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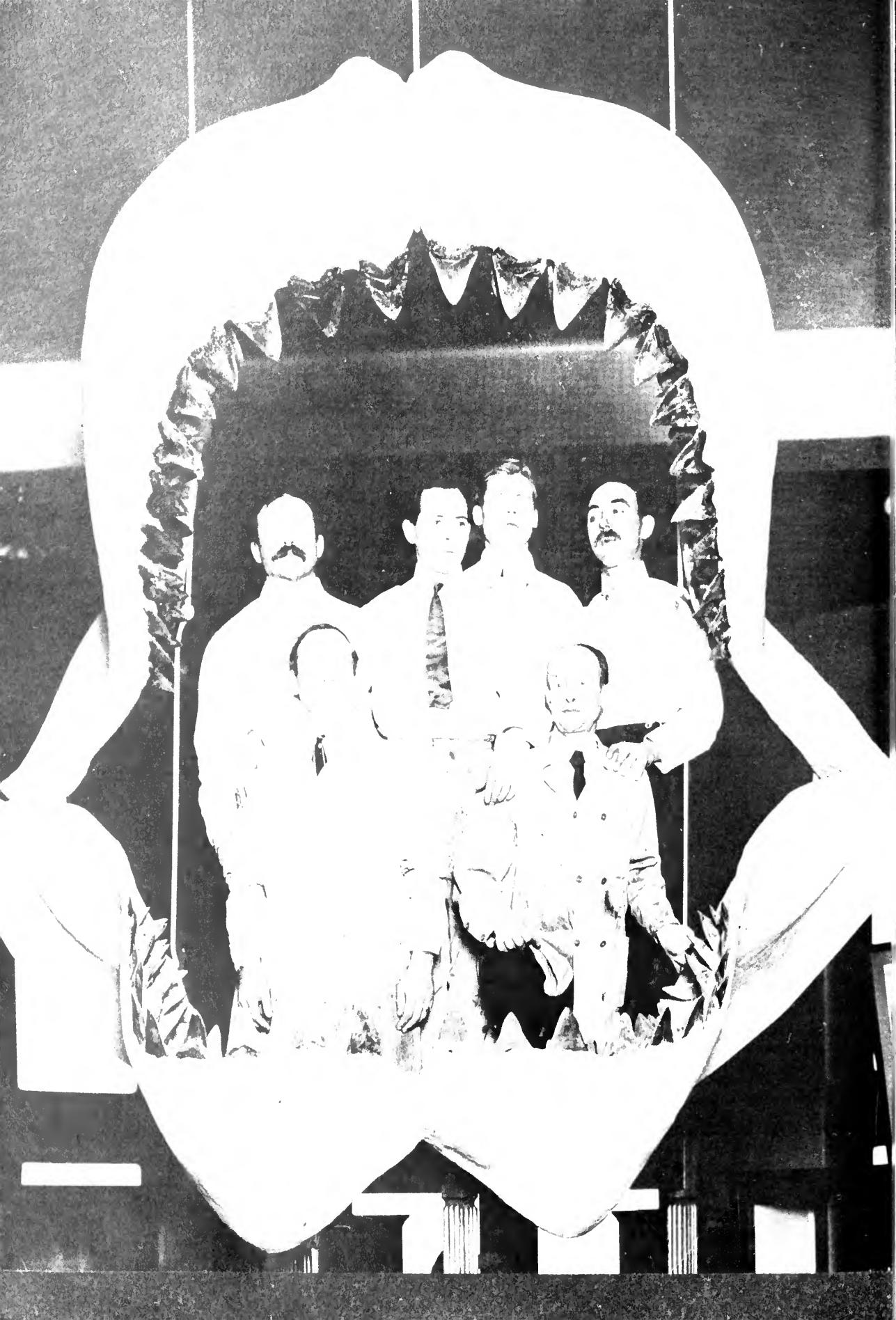
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Introduction



Photo by Flip Nicklin

From 1957 to 1977, there was a resurgence of interest in the basic biology and behavior of sharks, sparked by the United States Navy's commitment to the development of more effective shark deterrents. During these two decades more was learned about sharks than in the previous 200 years. It is reassuring to know that, in spite of diminished funding, a small but dedicated group of investigators still carries on, using imaginative approaches implemented by modern technology. Several of these investigators are represented in this issue of *Oceanus*, and their contributions are most timely and welcome.

The reader will find much new and exciting information about modern approaches to shark biology and behavior. Donald R. Nelson, A. Peter Klimley, and Paul R. Ryan report on field studies carried out in the open sea on several species of large sharks. Samuel H. Gruber's ambitious and

carefully conceived interdisciplinary approach to lemon shark energetics and biology, under both laboratory and field conditions, has already provided rewarding results. In a second short paper, Gruber summarizes preliminary experiments with pardaxin and detergent-like surfactants which repel sharks under laboratory conditions. Sanford A. Moss describes in some detail the various feeding mechanisms in sharks and correlates these with functional analyses of jaw movement and diet. Joel L. Cohen reviews the anatomy of the shark's visual system and remarks on the distribution of retinal rods and cones as well as visual projection centers in the brain. I describe the reproductive patterns of sharks and comment on their adaptive significance. Leonard J. V. Compagno presents a most welcome review of the major orders and families of living sharks and cites the ever-increasing number of described genera and species in each. While all the articles are deserving of extensive comment, I will call attention to only two, for historical reasons.

Compagno points out that more than 80 percent of the 300 to 350 species of sharks are less than 5 feet (average 1.6 meters) in length and that

the 32 species implicated in attacks on humans are of relatively large size (2.8 meters). These, coupled with 36 other species considered to be potentially dangerous, represent about 20 percent of the total species of living sharks.

Information on the number of attacks on humans on a worldwide basis in any given year is unfortunately incomplete. When Leonard P. Schultz and I started the International Shark Attack File (SAF) in 1957, we attempted to secure information on shark attacks from physicians, divers, scientists, and clipping services throughout the world, but this effort was only partially successful. Many areas known to be the scenes of frequent shark attacks, such as Indonesia, India, Central America, and South America, were only spottily represented. Of the 1,652 cases we were able to compile, H. D. Baldridge reduced 1,165 of these to a form usable by automatic data retrieval systems and concluded there was adequate documentation on 874 cases in which sharks were considered directly responsible for attacks on humans. Baldridge's thoughtful analysis was published in 1974 as "Contributions from the Mote Marine Laboratory, Volume 1, Number 2." At the same time, a widely acclaimed popular version of the report appeared as a Berkley Medallion Book in paperback entitled *Shark Attack*.

Based on the limited information in the SAF, Schultz and I concluded there were 30 to 50 recorded shark attacks per year on humans. Because we had so few records, or no records at all, for many of the shark-infested spots in the world, we estimated that at most there were less than 100 attacks on humans per year worldwide, and of these not more than 25 to 30 were fatal. Once the SAF (now under the direction of John J. McAniff, National Underwater Accident Data Center, University of Rhode Island, P.O. Box 68, Kingston, R.I., 02881) is reactivated this figure may increase for in Florida waters alone this year there have been 14 documented shark attacks, two of which were fatal. Bathers, boaters, and scuba divers, without being unduly alarmed, may well heed the advice Baldridge offers in this issue.

Gruber's article entitled "Shark Repellents: Perspectives for the Future" will probably evoke the most controversy in this issue and should be of great interest to those involved in seeking improved

shark deterrents. The exciting discovery by Dr. Eugenie Clark and her colleagues that a secretion of the Moses sole, *Pardachirus marmoratus*, inhibits the jaw movement of sharks has sparked the important line of investigations into the nature of the toxin, pardaxin. Gruber and Eliahu Zlotkin have carried these studies a step further and, under laboratory conditions, have found that certain relatively cheap industrial detergents were ten times more effective in repelling young lemon sharks than was the Moses sole extract. We all await with interest test results of these surfactants on dangerous sharks in the open sea. Lest we become too optimistic, it is well to bear in mind Baldridge's conclusion (in Seaman, 1976) that "incapacitation would probably be required for terminating preattack [shark] behavior by chemical means, and mathematical analyses clearly indicate that this is not likely to be realized in terms of realistic quantities of drugs and available exposure times." Meanwhile, we do have a wide variety of physical agents that are promising or have proved to be effective as shark deterrents (Gilbert, P. W., and C. Gilbert, 1973).

The studies presented in this issue are but a sampling of the exciting investigations currently under way. Reference to some of these investigations will be found in the selected readings at the end of each article or in other publications based on presentations at the 1976 New Orleans Shark Symposium and edited by R. Glenn Northcutt. As we gain an increased understanding of the basic biology and behavior of sharks, their use as biological models in medical research will certainly increase, and improved measures will be developed to protect humans and their gear in shark-infested waters.

Perry W. Gilbert

Selected Readings

- Gilbert, P. W., and C. Gilbert. 1973. Sharks and shark deterrents. *Underwater Journal*, 5: 69-79.
Northcutt, R. G., ed. 1977. Recent advances in the biology of sharks. *Amer. Zool.*, 17(2): 287-515.
Seaman, Wm., Jr., ed. 1976. Sharks and man: a perspective. Florida Sea Grant Report No. 10, pp i-iv, 1-36.

Legend Versus Reality:



The Jaws Image and Shark Diversity

by Leonard J. V. Compagno

The word "shark" calls up visions of large, toothy, dangerous marine monsters, rather like the protagonist of the novel and film *Jaws*. Many people may be familiar with sharks that do not fit this popular image, but the general impression that sharks can be typified by large and powerful species, such as the great white shark, persists in the public media and even in some scientific literature.

The large, formidable, predatory sharks are spectacular in appearance and noted for occasional attacks on human beings, but these are a decided minority among the approximately 350 species of sharks that inhabit the world's oceans and tropical rivers and lakes.

Most sharks are small and innocuous to humans. I recently compiled data on the total

lengths attained by 296 shark species. Of these, about 8 percent were dwarves, reaching between 20 and 40 centimeters long; 42 percent were small, between 40 centimeters and 1 meter; another 32 percent were of moderate size, between 1 and 2 meters; 6 percent were moderately large, between 2 and 3 meters; about 8 percent were large, between 3 and 4 meters; and the remaining 4 percent were 4+ meters long. In the sample, 82 percent of the species reached a maximum size in the range between 20 centimeters and 2 meters. An

*Above: although the great white shark, *Carcharodon carcharias*, epitomizes sharks to many people, it is unusual as a superpredator of great size, with exceptionally powerful jaws and teeth that enable it to prey on large marine vertebrates.*

average maximum adult size for these species was about 1.5 meters, or 4.9 feet, which is probably somewhat greater than a grand average of the mean adult size obtained by the species sampled.

Of about 32 species of sharks definitely identified in attacks on humans or boats, more than 80 percent are large species between 2 and 8+ meters long. Those sharks implicated in attacks on humans, and about 36 other species considered potentially dangerous, comprise about 20 percent of all species of sharks.

Although sharks are relatively common, shark attacks on people are not. According to H. David Baldridge, author of *Shark Attack*, shark attacks on a worldwide basis have averaged about 28 a year since 1940 and in no year up to 1974 surpassed 56. Data for Baldridge's study was from the International Shark Attack File (now discontinued) compiled by the United States Navy and the Smithsonian Institution. It included more than 1,600 examples of known shark attacks. Although it can be argued that this data base missed a certain number of shark attacks in the period covered, the impression one got from these records and other information is that the rate of shark attacks on people is minuscule compared to the massive rate of human attacks on sharks as reflected in fisheries statistics.

According to fisheries data gathered by the Food and Agriculture Organization of the United Nations and presented in *Shark Utilization and Marketing* by R. Kreuzer and R. Ahmed, the world shark catch for 1976 was about 307,085 metric tons. If the average shark in this catch weighed — say 68 kilos or 150 pounds — the catch would be equivalent to sharks “catching” 4.5 million people! Clearly, sharks have far more to fear from people than vice versa.

8 Major Taxonomic Groups

Living sharks fall into eight major taxonomic groups, or orders, of grossly unequal size but great antiquity. Most of these date back as fossils to the Jurassic period of the Mesozoic era, between 130 and 180 million years ago. New finds may push the living shark orders even further back in time. Sharks and their relatives, the rays, form one of numerous major phyletic branches of the class Chondrichthyes, or cartilaginous fishes. Fossil shark-like fishes first appeared in the Devonian period of the Paleozoic era, between 340 and 400 million years ago. They subsequently evolved into many divergent groups of cartilaginous fishes. Only two of these groups, the neoselachians (comprising the eight orders of living sharks and the rays) and the holocephalians (chimaeras, ratfishes, and elephant fishes) survive at present. Most of the other groups of cartilaginous fishes became extinct at the end of the Permian period and Paleozoic era, about 230 million years ago.

The diversity of living sharks is indicated in Table 1, which lists orders, families, and genera of living sharks. Numbers of species are presented parenthetically after each genus and order, and separately for each family with two or more genera. The numbers are from a checklist of world sharks I am preparing for publication by the Food and Agriculture Organization. It represents a revision over earlier numbers published in my article on shark phyletics (Compagno, 1977). The species numbers given after families and orders represent minimum numbers of valid species recognized at this time. Since systematics at the species level is still in a state of flux for many higher groups of sharks, it is to be expected that these species numbers will change as some described species are synonymized with others and new species are discovered.

The frilled shark, Chlamydoselachus anguineus, is a deep-water, eel-like hexanchoid with poorly known habits. Its long, snake-like mouth, tricuspid teeth, and enlarged, pointed denticles on its lips may help it to capture slippery prey, such as squid.



Table 1. Orders, families, and genera of living sharks.

ORDER HEXANCHIFORMES (5+). Hexanchoid sharks.

Family Hexanchidae (six-gill and seven-gill sharks): *Heptanchias* (1+), *Hexanchus* (2), *Notorynchus* (1); (5+).
Family Chlamydoselachidae (frilled sharks): *Chlamydoselachus* (1).

ORDER SQUALIFORMES (70+). Squaloid, or dogfish, sharks.

Family Echinorhinidae (prickly sharks): *Echinorhinus* (2).
Family Squalidae (dogfish sharks): *Aculeola* (1), *Centrophorus* (8+), *Centroscyllium* (6), *Centroscymnus* (5-7), *Cirrhigaleus* (1),
Dalatias (1), *Deania* (3), *Etmopterus* (18+), *Euprotomicrodes* (1), *Heteroscymnoides* (1), *Isistius* (2),
Scyrnodalatias (1), *Scymnodon* (3-4), *Somniosus* (3+?), *Squaliolus* (1), *Squalus* (7+); (64+).
Family Oxynotidae (rough sharks): *Oxynotus* (4-5?).

ORDER PRISTIOPHORIFORMES (5+). Pristiophoroid sharks.

Family Pristiophoridae (sawsharks): *Pliotrema* (1), *Pristiophorus* (4-5+); (5+).

ORDER SQUATINIFORMES (12+). Squatinoid sharks.

Family Squatinidae (angel sharks): *Squatina* (12-13?).

ORDER HETERODONTIFORMES (8). Heterodontoid or bullhead sharks.

Family Heterodontidae (bullhead sharks): *Heterodontus* (8).

ORDER ORECTOLOBIFORMES (27+). Orectoloboid or carpet sharks.

Family Parascyllidae (collared carpet sharks): *Cirrhoscyllium* (1-3?), *Parascyllium* (4); (5+).
Family Brachaeluridae (blind sharks): *Brachaelurus* (1), *Heteroscyllium* (1); (2).
Family Orectolobidae (wobbegongs): *Eucrossorhinus* (1-2?), *Orectolobus* (5); (6+).
Family Hemiscylliidae (long-tailed carpet sharks): *Chiloscyllium* (4+?), *Hemiscyllium* (5); (9+).
Family Ginglymostomatidae (nurse sharks): *Ginglymostoma* (2), *Nebrius* (1-2?); (3+).
Family Stegostomatidae (zebra sharks): *Stegostoma* (1?).
Family Rhiniodontidae (whale sharks): *Rhincodon* (1).*

ORDER LAMNIFORMES (14+). Lamnid sharks.

Family Odontaspididae (sand tiger sharks): *Eugomphodus* (1-2?), *Odontaspis* (1-2?); (2+).
Family Pseudocarchariidae (crocodile sharks): *Pseudocarcharias* (1).
Family Mitsukurinidae (goblin sharks): *Mitsukurina* (1).
Family Alopiidae (thresher sharks): *Alopias* (3).
Family Cetorhinidae (basking sharks): *Cetorhinus* (1?).
Family Lamnidae (mackerel sharks): *Carcharodon* (1), *Isurus* (2), *Lamna* (2); (5).
Family (unnamed, for "megamouth" shark; 1).

ORDER CARCHARHINIFORMES (199+). Carcharhinoid, or carcharhiniform, sharks.

Family Scyliorhinidae (catsharks): *Apristurus* (25+), *Asymbolus* (1), *Atelomycterus* (2+), *Aulohalaelurus* (1), *Cephaloscyllium* (5+), *Cephalurus* (1+), *Galeus* (10), *Halaelurus* (10), *Haploblepharus* (3), *Holohalaelurus* (2), *Juncrus* (1), *Parmaturus* (4), *Pentanchus* (1), *Poroderma* (3), *Schroederichthys* (4), *Scyliorhinus* (14); (87+).
Family Proscylliidae (finback catsharks): *Ctenacis* (1), *Eridacnis* (3+?), *Gollum* (1), *Proscyllium* (1+?); (6+).
Family Pseudotriakidae (false catsharks): *Pseudotriakis* (2?).
Family Leptochariidae (slender houndsharks): *Leptocharias* (1).
Family Triakidae (houndsharks): *Furgaleus* (?), *Galeorhinus* (1?), *Gogolia* (1), *Hemitriakis* (2-3?), *Hypogaleus* (1), *Iago* (3), *Mustelus* (24), *Scylliogaleus* (1), *Triakis* (5); (39+).
Family Hemigaleidae (weasel sharks): *Chaenogaleus* (1), *Hemigaleus* (1), *Hemipristis* (1), *Paragaleus* (3+?): (6+).
Family Carcharhinidae (requiem sharks): *Carcharhinus* (32+?), *Galeocerdo* (1?), *Isogomphodon* (1), *Lamiopsis* (1), *Loxodon* (1), *Negaprion* (2), *Prionace* (1), *Rhizoprionodon* (7?), *Scoliodon* (1), *Triaenodon* (2); (49).
Family Sphyrnidae (hammerhead sharks): *Eusphyra* (1), *Sphyra* (8); (9).

*The spelling of this genus name is in dispute. A ruling on the matter is forthcoming from the International Commission on Zoological Nomenclature.

Table 2. Numbers of families, genera, and species of living sharks.

	Families Nos.	Families %	Genera Nos.	Genera %	Species (Minimum) Nos.	Species (Minimum) %
Order Hexanchiformes	2	6.7	4	4.2	5	1.5
Order Squaliformes	3	10.0	19	19.8	70	20.3
Order Pristiophoriformes	1	3.3	2	2.1	5	1.5
Order Squatiniformes	1	3.3	1	1.0	12	3.5
Order Heterodontiformes	1	3.3	1	1.0	8	2.3
Order Orectolobiformes	7	23.3	12	12.5	27	7.8
Order Lamniformes	7	23.3	10	10.4	14	4.1
Order Carcharhiniformes	8	26.7	47	49.0	199	57.8
Totals:	30	100.0	96	100.0	340	100.0

The numbers in Table 1 include a few undescribed species of *Iago* (2) and *Mustelus* (4) in the Triakidae, and of *Paragaleus* (1) in the Hemigaleidae; and the undescribed family, genus, and species for the bizarre megamouth shark. The classification follows my paper in *Interrelationships of Fishes* (Compagno, 1973).

The eight shark orders, using the criteria of relative numbers of genera, species, and morphological diversity, fall into three categories: the minor groups, the major groups, and the dominant group (Table 2). The minor groups—orders Hexanchiformes, Pristiophoriformes, Squatiniformes, and Heterodontiformes—are relatively undiverse, representing relatively small, if highly distinctive, adaptive radiations during their history. The Hexanchiformes were formerly more varied than at present, but it is doubtful if they ever approached the present diversity of the Squaliformes at any period in their history. The Pristiophoriformes, Squatiniformes, and Heterodontiformes are essentially monomorphic groups, with very little past and present diversity.

The major but nondominant orders of Squaliformes, Orectolobiformes, and Lamniformes are presently quite diverse in families and genera (the families of Squaliformes are possibly undersplit as presently recognized), but are far inferior to the dominant order Carcharhiniformes in numbers of genera and species.

The major and dominant groups represent large adaptive radiations, with dozens of genera and numerous species. The Lamniformes was formerly far more diverse in genera and species in the late Mesozoic and early Cenozoic, but shows an apparent decline in numbers of genera and especially in species since the mid-Cenozoic (possibly due to competition with advanced Carcharhiniformes).

The Orectolobiformes retains more species, but its greatest generic and specific diversity is confined to the Indo-West Pacific—especially the

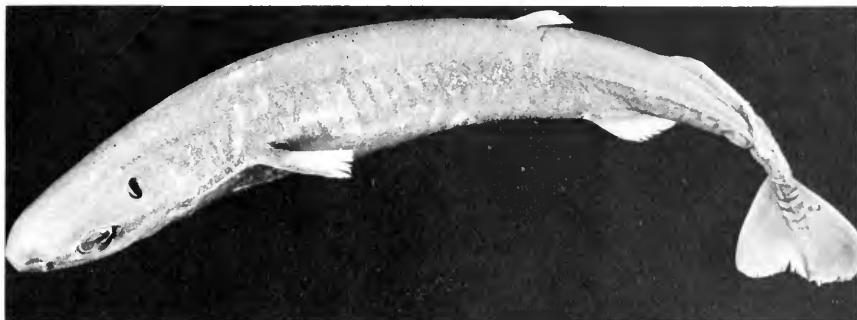
Australian region, where 10 of the 12 orectoloboid genera and most of the species occur (versus six genera from the rest of the Indo-West Pacific and only two genera in the Atlantic and eastern Pacific). The Squaliformes has a large number of species, but these mostly complement the Carcharhiniformes by occurring in habitats with moderate or low carcharhinoid diversity, such as the upper continental slopes, higher latitudes, and ocean basins.

The order Carcharhiniformes predominates in genera, species, and shark biomass in the habitats probably optimal for shark diversity. These include the continental and insular shelves of warm temperate and tropical marine waters, the upper continental slope (primarily Scyliorhinidae), and a few species that enter tropical and temperate rivers and lakes. Fisheries surveys of tropical and warm temperate shelf and oceanic environments typically yield about 96 percent carcharhinoids by number of individuals compared to other sharks.

With the possible exception of the hammerhead sharks, the Carcharhiniformes includes few really specialized sharks with unusual trophic adaptations or other peculiarities. The hammerheads are essentially carcharhinid derivatives with their prebranchial heads modified as flattened bowplanes (see page 65).

The Squaliformes includes highly specialized pelagic genera—*Euprotomicrus*, *Squaliolus*, *Euprotomicroides*, *Heteroscymnoides*, and especially the semiparasitic "cookie-cutter" sharks, genus *Isistius*. It also includes genera with bizarre body forms (*Deania*, *Oxynotus*), many genera and species with luminous organs, and a genus (*Somniosus*) with species dwelling in arctic and subantarctic cold.

The Orectolobiformes includes bottom-dwelling specialists, such as the flat, anglerfish-like wobbegongs (Orectolobidae), slender, crevice-loving hemiscylliids with limb-like paired fins, the anatomically divergent parascylliids,



Several squaloid sharks, including this pygmy shark, *Euprotomicrus bispinatus*, are oceanic and have minute, scattered luminescent organs on their bodies. This species is wide-ranging in warm oceanic waters, reaches a maximum length of 27 centimeters, and may migrate from the surface to the bottom in a daily cycle.

and the genus *Stegostoma* with a caudal fin about as long as the rest of the shark, but also the pelagic, filter-feeding whale shark.

The small, but highly diverse, order *Lamniformes* includes two types of pelagic filter-feeders, probably separately evolved — the megamouth and the basking sharks — the long-tailed thresher sharks (using their elongated caudal fins as weapons for feeding), the grotesque goblin shark, the oceanic crocodile shark, the high-speed shortfin mako (*Isurus oxyrinchus*), and the superpredatory great white shark.

The reasons for the preeminence of the *Carcharhiniformes* among modern sharks and the greater morphological variety within the three major groups are unclear. The implication is that carcharhinoids are competitively superior to other sharks. The advanced carcharhinoid families, such as the *Hemigaleidae*, *Carcharhinidae*, and *Sphyrnidae*, may have more efficient feeding mechanisms (jaws, hyoid arch, and musculature) and reproduction (placental viviparity) than noncarcharhinoids and more primitive carcharhinoids. The wide morphological diversity among lamnoids, orectoloboids, and squaloids may be due to competitive exclusion of these groups from more generalized shark niches by carcharhinoids, optimizing their evolution into more peripheral specialists. However, all this is speculative, and there may be other, more compelling reasons that explain the relative numbers and comparative morphological variation of the *Carcharhiniformes* and other shark groups.

A Review of Living Sharks

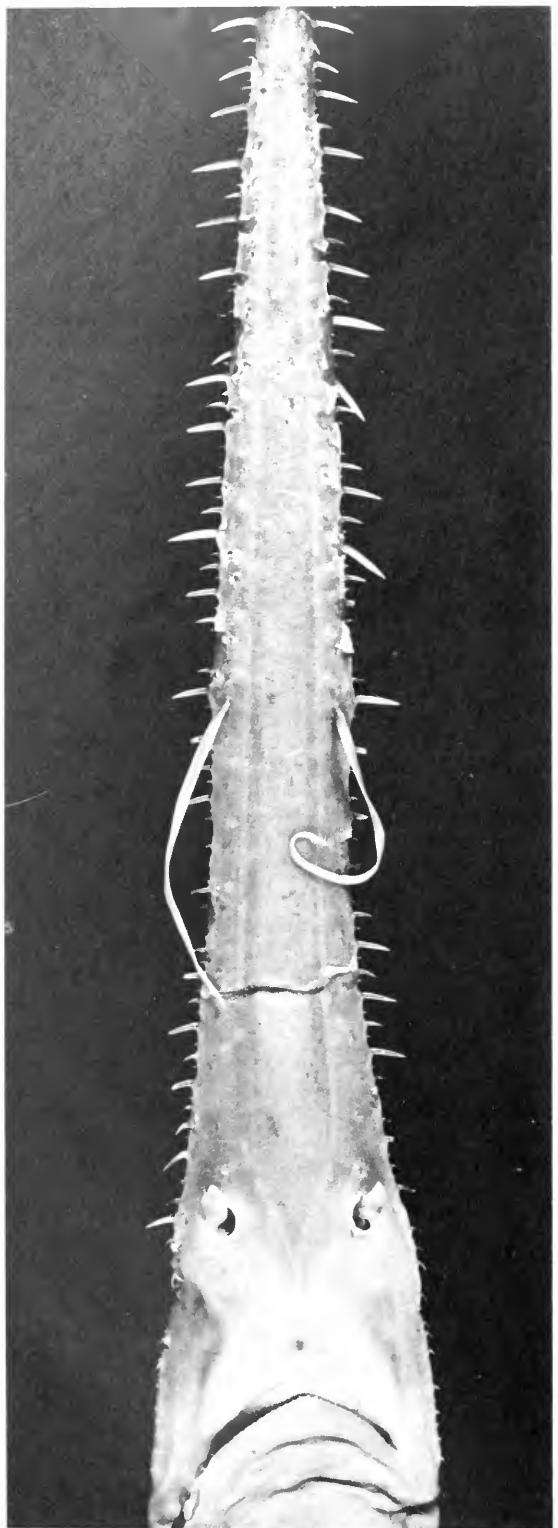
Unfortunately, very little is known of the basic biology of most sharks, and much of the research on sharks has been concentrated on species, such as the spiny dogfish (*Squalus acanthias*), that occur in northern temperate waters and are objects of important fisheries.

The *Hexanchiformes*, or hexanchoid sharks, are easily identified by their single, spineless dorsal fin, anal fin, and six or seven pairs of gill openings (all other sharks have five, except the six-gill sawshark, *Pliotrema*). Hexanchoids are primarily

deep-water, bottom-dwelling, temperate-to-tropical, continental or insular sharks with a worldwide distribution and a depth range from close inshore to at least 1,875 meters. The rare frilled shark, *Chlamydoselachus*, is elongated and eel-shaped, with small tricuspid teeth in both jaws and a terminal mouth. The six-gill and seven-gill sharks, *Hexanchidae*, have stouter bodies, large, comb-like slicing teeth in the lower jaw, and a subterminal mouth. Frilled sharks reach 196 centimeters in length, while six-gill and seven-gill sharks range from 137 to 482 centimeters long. Virtually nothing is known of the frilled shark's habits, except that it may feed on squid, but the six-gill and seven-gill sharks are known to take a wide variety of bony fishes, other sharks, rays, crustaceans, and carrion for food. All hexanchoids are aplacentally viviparous, bearing live young. Some of the larger species, including the broadnosed six-gill (*Hexanchus griseus*) and seven-gill (*Notorynchus cepedianus*) sharks, are excellent for food.



The large-tooth cookie-cutter shark, *Isistius plutodus*, has suctional lips for clinging to its prey. This shark has the largest teeth relative to its size of any living shark, about twice the tooth height to total length ratio of the great white shark (the species with the physically largest teeth of any living shark), but reaches a total length of only 42 centimeters.



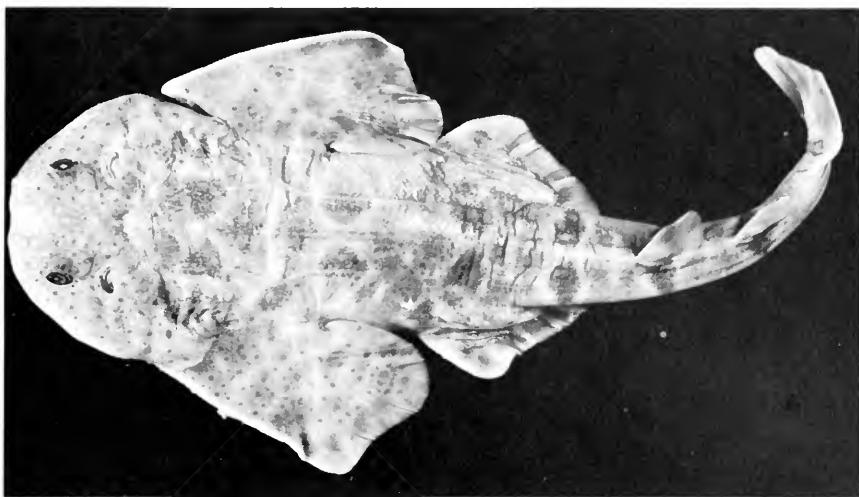
Head of a Philippine sawshark, *Pristiophorus* sp., from the underside, showing its saw-like snout and rostral barbels.

The Squaliformes, or dogfish sharks, are cylindrical, compressed, or slightly flattened sharks with two spined or spineless dorsal fins and no anal fin. Like the hexanchoids, squaloid sharks are mainly inhabitants of deep water near the bottom, from the continental shelves down to at least 2,700 meters on the slopes and possibly also occurring on the ocean floor. Several squaloids are pelagic over the ocean basins, and the common spiny dogfish, *Squalus acanthias*, and large sleeper sharks, *Somniosus microcephalus* and *S. pacificus*, can occur close inshore and even intertidally. Small unicuspis or tricuspid teeth occur in both jaws of a few squaloids (*Aculeola*, *Centroscyllium*), but most squaloids have enlarged, compressed, blade-like teeth in the lower jaw or both jaws. The extreme in blade-like cutting teeth is seen in the lower jaws of the cookie-cutter sharks (*Isistius*), one species of which (*I. plutodus*) has the largest teeth in proportion to body size of any living shark.

Many of the deep-water squaloids are blackish or dark brown in color, and commonly have small luminous organs scattered on the body or in well-marked areas. The majority of squaloids reach lengths of between 30 and 170 centimeters, but there are several dwarf species below 30 centimeters and one, *Squaliolus laticaudus*, that may be the smallest shark, maturing at 15 to 26 centimeters. In contrast, the large prickly and bramble sharks, *Echinorhinus*, reach 3 to 4 meters, and the large sleeper sharks may exceed 7 meters. Deep-water squaloids often have very long bodies, with immense livers serving as hydrostatic organs.

Squaloids usually have cylindrical or moderately compressed bodies, but the rough sharks, *Oxynotus*, have high bodies with a triangular cross section and high, sail-like dorsal fins. Squaloids eat a wide variety of fish, other sharks, rays, crustaceans, and cephalopods. The cookie-cutter sharks are semiparasitic, with suctorial lips that enable them to attach to large bony fishes and cetaceans and core out a plug of flesh with their huge teeth; they also feed on small fishes and squid. All squaloids are aplacentally viviparous. A number of dogfish sharks are commercially important, especially the spiny dogfish and the sleeper sharks, supporting large fisheries. Deep-sea dogfish are prized for the squalene in their livers, which, among other things, is used as a base for cosmetics. Squaloid sharks are generally not considered dangerous to people, but the sharp teeth and weakly toxic fin spines of some species can inflict injuries.

The Pristiophoriformes, or sawsharks, have two dorsal fins and no anal fin like squaloids, but differ in their greatly attenuated, blade-like snouts with lateral teeth and long barbels on the undersides. One sawshark, *Pliotrema warreni*, has six pairs of gill openings, but the others, genus *Pristiophorus*, have only five. Sawsharks favor



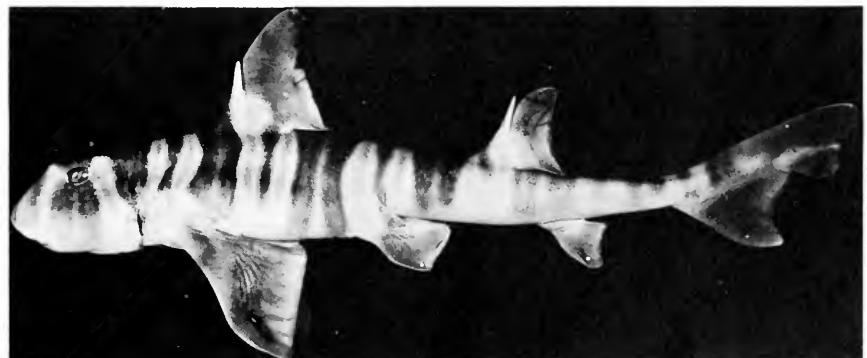
The California angel shark, *Squatina californica*, a depressed, ray-like bottom shark of the eastern Pacific.

warm-temperate-to-tropical waters and occur in the western Indian Ocean, western Pacific, and western North Atlantic in the vicinity of Cuba and the Bahamas. These sharks are little-known bottom-dwellers of the continental shelves and upper slopes at depths from 18 to 951 meters. Presumably these small (80-140 centimeters) sawsharks use their saw-like snouts to disable small fishes and crustaceans, as do the larger sawfishes, Pristidae, but this has never been observed. Sawsharks are live-bearing (aplacentially viviparous). A considerable fishery for sawsharks exists off southern Australia.

The Squatiniformes, or angel sharks, are greatly flattened, bottom-dwelling, ray-like sharks with an expanded oval head, large pectoral fins with short, triangular lobes covering the gill openings, no anal fin, and a unique caudal fin with the lower lobe longer than the upper. These cold-temperate-to-tropical sharks are found in the Atlantic, southwestern Indian Ocean, and Pacific Ocean, on the continental shelves and upper slopes, from close inshore down to possibly 1,289 meters.

Angel sharks often bury themselves in sandy or muddy bottoms, lurking like anglerfish to suck and grab small fish and crustacea with their protrusible jaws and small, needle-sharp impaling teeth. Angel sharks are live-bearing and reach a length of 108 to 200 or more centimeters. Several angel shark species are fished for human consumption and also are used for fishmeal and other fish products. They can inflict serious lacerations when provoked.

The Heterodontiformes, or bullhead sharks, are the only living sharks that have two spined dorsal fins and an anal fin. They have prominent crests above the eyes, small, piglike snouts with the nostrils and mouth connected by deep grooves, and eyes that are well behind the mouth. Their teeth are peculiar — small and cuspidate at the front of the mouth, but large and molariform in back. Bullhead sharks are found in shallow, warm-temperate-to-tropical seas, often close inshore on the continental shelf, but ranging down to 275 meters. These sharks presently have a restricted geographic range in the western Indian Ocean, western Pacific, and eastern Pacific, but



Bullhead sharks are the only living sharks with spined dorsal fins and an anal fin. This zebra bullhead shark, *Heterodontus zebra*, occurs in the western Pacific.



This nurse shark, *Ginglymostoma cirratum*, shows the pig-like snout, small anterior mouth in front of the eyes, and nasal barbels characteristic of orectoloboid sharks.

formerly inhabited the Atlantic. Many species favor rocky areas with reefs and crevices, where they slowly swim just above the bottom or clamber across it on their muscular paired fins.

Bullhead sharks eat much hard-shelled invertebrate prey, including crustaceans, molluscs, and echinoderms (especially sea urchins), but they also eat small fishes; their large rear teeth enable them to crush prey without difficulty. These sharks lay eggs (oviparous) in conical egg cases with unique spiral flanges. Although of little interest to commercial fisheries, bullhead sharks are occasionally taken by sportfishermen and often by divers. They may bite when provoked but are considered harmless.

The Orectolobiformes, or carpet sharks, resemble bullhead sharks in their piglike snouts, grooves between nostrils and mouth, eyes behind the mouth, and two dorsal fins and an anal fin, but they lack dorsal spines and usually have nasal barbels. Most have small, cuspidate impaling and crushing teeth, but the wobbegongs (Orectolobidae) have enlarged, fang-like teeth and the tawny shark, *Nebrius*, has blade-like teeth. All are warm-temperate-to-tropical sharks of shallow to moderate depths on the continental shelves or in the upper layer of the oceans, ranging down to 183 meters. Almost all of the carpet sharks are bottom dwellers, except for the pelagic whale shark, *Rhincodon typus*.

Some carpet sharks are specialized for bottom dwelling. The long-tailed carpet sharks (Hemiscylliidae) have muscular paired fins that help them move on coral and rocky reefs, and the wobbegongs (Orectolobidae) have a camouflage of dermal flaps along the head and a variegated color pattern. Like the angel sharks (Squatinidae), the wobbegongs are bottom lurkers—often half buried in sand or blending in rock or coral—that ambush bottom prey.

Most carpet sharks eat small fishes and invertebrates and are helped by the bellows-like arrangement of their small mouths and large oral cavities, which enable them to suck in prey. Some of these sharks can expel water from their mouths in a strong stream, sometimes in the faces of fishermen who catch them.

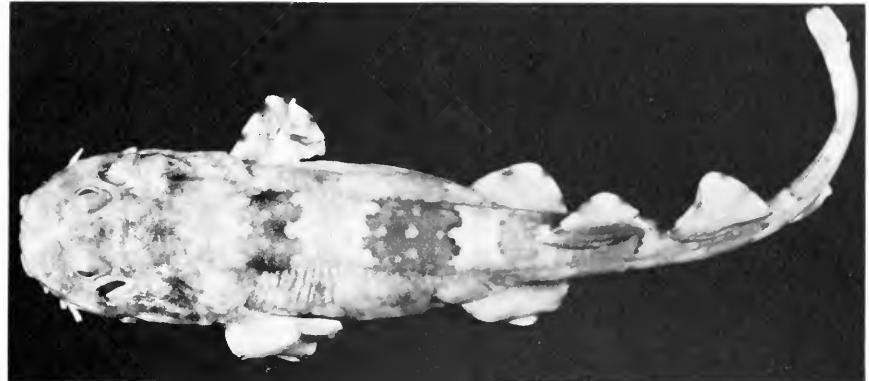
The huge whale shark has grid-like gill filters that enable it to strain plankton and small fish while swimming horizontally, but it also feeds vertically, with its head at the surface in a school of small fish, by raising its head and draining its oral cavity through the gills, then lowering its head with open mouth to let water and fish pour in.

The smaller carpet sharks (Parascylliidae, Brachaeluridae, Hemiscylliidae) grow 1 meter long at most, but others (Stegostomatidae, Ginglymostomatidae, Orectolobidae) attain 3 or more meters in length. The whale shark, the largest living fish, may reach 18 to 21 meters (based on sight records of huge individuals).

Orectoloboid sharks either lay eggs in oval or conical egg cases without spiral flanges or are live-bearing. The carpet sharks are fished commercially as well as by sportfishermen and divers. Nurse sharks (Ginglymostomatidae), some long-tailed carpet sharks, *Chiloscyllium*, and zebra sharks, *Stegostoma*, are commonly consumed for food. One nurse shark, *Ginglymostoma cirratum*, is prized for the leather made from its tough hide. The whale shark is harpooned for food in India and may be fished in China. The larger orectoloboids, especially nurse sharks and wobbegongs, can be dangerous when provoked and sometimes attack people unprovoked; the whale shark is usually harmless, but has infrequently rammed boats (usually boats and ships ram it instead).

The Lamniformes, or lamnid sharks, are “typical sharks,” with long mouths, conical or flattened snouts, two dorsal fins without spines, an

The Australian ornate wobbegong, *Orectolobus ornatus*, a bottom-dwelling orectoloboid shark camouflaged with flaps of skin on the sides of its head and a variegated color pattern.



anal fin, eyes over the mouth, and nostrils separate from the mouth. Most have enlarged teeth in the front of the mouth, separated from more rearward teeth by small intermediate teeth in the upper jaw that divide the dentition into impaling and slicing areas. Lamnoid sharks are found in tropical-to-cold-temperate and boreal waters. Some species are oceanic and epipelagic, some coastal-pelagic on the continental shelves, and others are found near the bottom on the continental slopes, down to below 1,000 meters. Almost all of the lamnoids are large or very large sharks, reaching a maximum size of 4 meters or more.

The small, oceanic crocodile shark, *Pseudocarcharias*, is exceptional in attaining only 1.2 meters in length, but the great white shark may reach between 6 to 9 meters and the basking shark 10 to 14 meters. Most lamnoids eat fishes, other sharks, crustaceans, and cephalopods, but the great white shark also eats marine mammals, especially pinnipeds, and the basking and megamouth sharks eat plankton. Most lamnoids are firm-bodied and probably strong swimmers, but the deep-water goblin shark may be an exception. The long, blade-like snout, very slender teeth, soft, flabby body, low, rounded fins, and unforked caudal fin of the goblin shark suggest that it is a slow, weak-swimming bottom-lurker, ambushing small fishes, crustaceans, and cephalopods with its highly protrusible jaws.

The sand tiger sharks (Odontaspidae) are generalized large coastal and insular sharks that feed largely on bony fishes. The crocodile shark and longfin mako shark, *Isurus paucus*, are oceanic species, probably feeding mainly on fish and squid.

The megamouth shark is a tropical, oceanic plankton feeder, with gill rakers formed from finger-like dermal papillae and a huge, small-toothed mouth apparently rimmed by luminous gum tissue; only a single specimen is known, captured in the vicinity of the Hawaiian Islands.

The basking shark is another lamnid filter-feeder (its relation to megamouth is unclear), with gill rakers formed of bristle-like placoid scales and a bipolar distribution in temperate coastal waters.

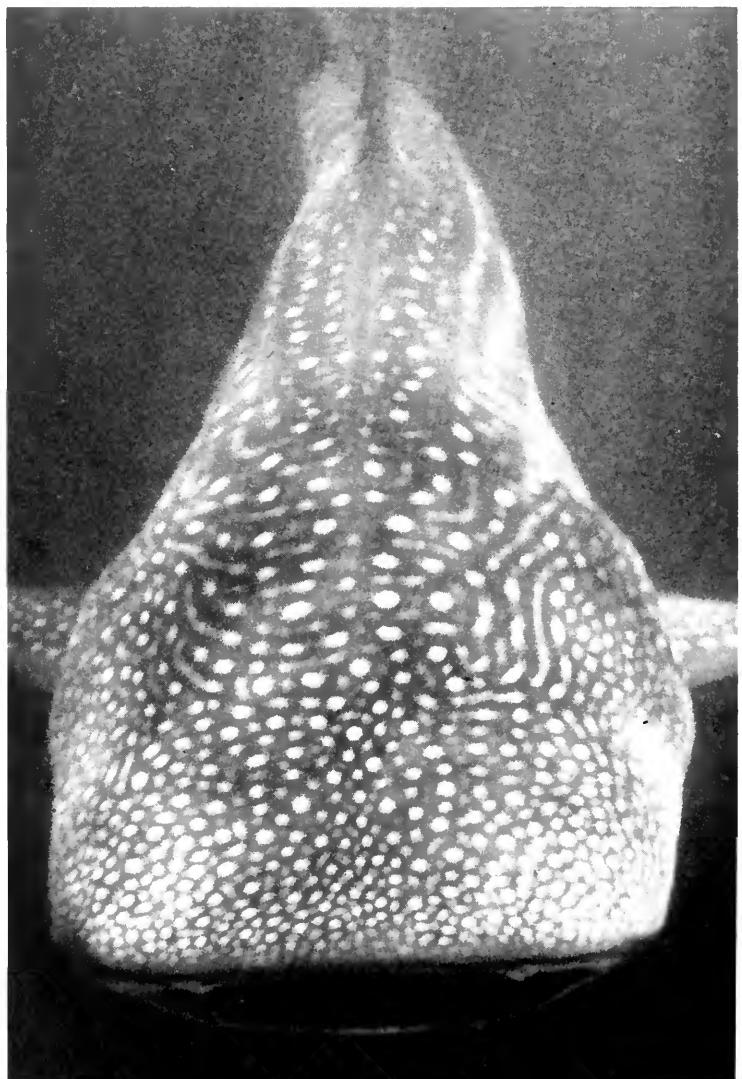
The shortfin mako, *Isurus oxyrinchus*, porbeagle, and salmon sharks, *Lamna*, are coastal-oceanic, primarily fish and squid eaters. The great white shark is a coastal superpredator with a wide food range, possibly biased in larger individuals toward marine mammals, but toward bony fish, other sharks, and even invertebrates in smaller ones. The mackerel sharks, *Lamnidae*, are partially homoiothermic, or warm-blooded, with countercurrent networks of blood vessels in their body muscles that increase muscle power; their spindle-shaped bodies, strongly horizontal tail keels, and crescentic caudal fins make them powerful swimmers.

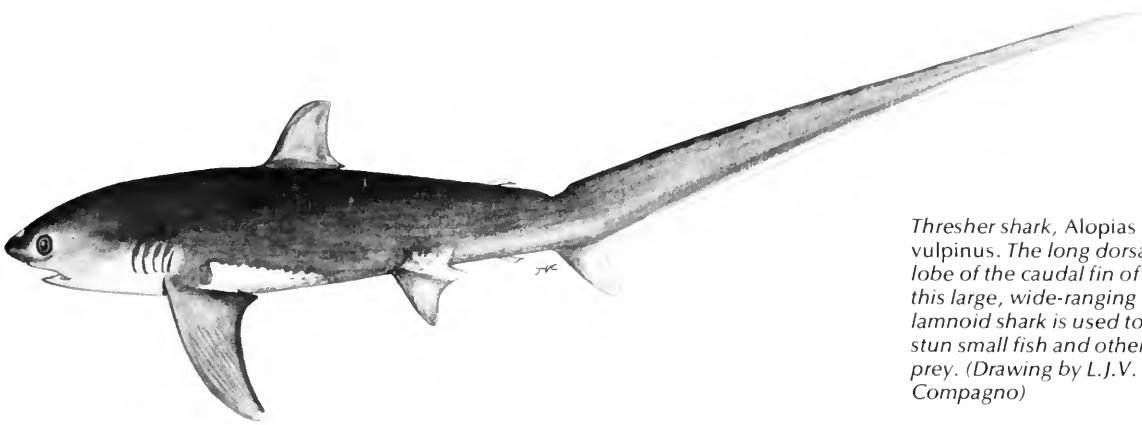


The crocodile shark, *Pseudocarcharias kamoharai*, a small (to 110 centimeters) oceanic lamnid with highly protrusible jaws and slender, hook-like teeth.



Three plankton-feeders.
Left — a 7-meter basking
shark, *Cetorhinus*
maximus. (Photo by
Chuck Davis) Below left —
the taxonomically
unclassified
“megamouth” shark,
caught at a depth of 150
meters near Hawaii. (U.S.
Navy photo) Below — a
whale shark, *Rhincodon*
typus, the largest fish.
(Photo by Jeremiah S.
Sullivan)





Thresher shark, Alopis vulpinus. The long dorsal lobe of the caudal fin of this large, wide-ranging lamnid shark is used to stun small fish and other prey. (Drawing by L.J.V. Compagno)

The shortfin mako is outstanding in its speed and in its ability to leap marlin-like from the water; it may be the fastest-swimming shark. The thresher sharks, *Alopis*, are coastal and oceanic sharks that use their extremely elongated upper caudal fins as whips to strike and stun small fish.

Some lamnoids are noted for uterine cannibalism, in which a developing fetus in the uterus devours its potential siblings in the form of eggs from the ovary. Many lamnoids are important food fishes and support significant fisheries, especially the mackerel, thresher, and sand tiger sharks; the basking shark has been sporadically fished for its liver, meat, and other products. The great white shark and shortfin mako are implicated in many attacks on swimmers, divers, and boats.

Last but hardly least are the Carcharhiniformes, "typical sharks" with long mouths, two dorsal fins without spines, an anal fin, and the eyes over the mouth, but differing from the lamnoids in having movable lower eyelids. These sharks swarm in the tropics, are very common in temperate coastal waters, are found on the continental and insular slopes down to at least 2,000 meters, and, in the form of a few species of large carcharhinid sharks, such as the blue shark, *Prionace glauca*, and silky and oceanic whitetip sharks, *Carcharhinus falciformis* and *C. longimanus*, in the upper levels of the ocean basins. Most carcharhinoids are small, below 2 meters in length, but the requiem and hammerhead sharks have many large species more than 2 meters long (two of which, the tiger shark, *Galeocerdo cuvier*, and the great hammerhead, *Sphyrna mokarran*, exceed 5.5 meters). On the other hand, the catsharks (Scyliorhinidae and Proscylliidae) have several species not exceeding 30 centimeters, with one, *Eridacnis radcliffei*, being among the smallest known sharks at 19 to 24 centimeters.

Carcharhinoid sharks eat a wide variety of bony fishes, sharks, rays, invertebrates, and carrion. Some of the houndsharks (Triakidae) feed

heavily on crustaceans, and the tiger shark is remarkably indiscriminate in its feeding, often swallowing garbage as well as oddities such as sea snakes, marine turtles, and conch shells. The carcharhinoids are a varied but relatively homogeneous group, and carcharhinoid families are for the most part not easy to distinguish (unlike lamnid families). There is a morphological gradient in this group, ranging from the small, weak-swimming, small-toothed scyliorhinid catsharks through intermediate families (Proscylliidae, Pseudotriakidae, Leptochariidae, Triakidae, and Hemigaleidae) to the large, strong-swimming, large-toothed requiem and hammerhead sharks.

The catsharks (Scyliorhinidae and Proscylliidae) are small, mainly upper-slope and outer-shelf species that are also found in shallow water. The false catsharks, *Pseudotriakis*, are large (to about 3 meters), deep-water species rivalled by the whale, megamouth, and basking sharks in number of teeth but differing in diet from these filter-feeders (one was photographed underwater while swallowing a large bony fish).

The houndsharks (Leptochariidae and Triakidae) and weasel sharks (Hemigaleidae) are small to moderately large (usually less than 2 meters) fish- and invertebrate-feeding sharks that are common close inshore, primarily in the tropics.

The large requiem shark family (Carcharhinidae) includes many large and dangerous species as well as common well-known smaller forms. These include the bull, dusky, blacktipped, gray reef, bronze whaler, oceanic whitetip, Galápagos, and silvertip sharks (*Carcharhinus*), blue sharks (*Prionace*), tiger sharks (*Galeocerdo*), lemon sharks (*Negaprion*), sharpnosed sharks (*Rhizoprionodon*), and the reef whitetip shark (*Triaenodon*).

The hammerhead sharks are very similar to the requiem sharks, but have a unique bowplane, formed from the sides of the head, apparently



Some carcharhinoids are among the smallest living sharks. This Philippine ribbontail catshark, *Eridacnis radcliffei*, is mature at a length of 19 to 24 centimeters. The upper left shark is a 23-centimeter pregnant female, from which the center 11-centimeter full-term fetus was removed; the lower right adult male is 22 centimeters long.



Hammerhead sharks have the prebranchial head expanded laterally as a flat hydrofoil that presumably increases their ability to maneuver. The extreme among hammerheads is this winghead shark, *Eusphyra blochii*, from the Indian Ocean and western Pacific, which has a head width 40 to 50 percent of its total length.

equipping these sharks for fast maneuvering; the wings of the bowplane are supported by special expansions of the orbital and nasal regions of the cranium.

Many carcharhinoids are live-bearing. Some are aplacentally viviparous, but a large number have placental viviparity, with yolk-sac placentas formed from the fetal yolk sac and the maternal uterine wall. Most scyliorhinid catsharks and one finbacked catshark, *Proscyllium*, are oviparous, and lay eggs in rectangular egg cases with corner tendrils.

Many carcharhinoid sharks support important fisheries for food and fish products such as fishmeal, liver oil, and leather. The most significant fisheries are for some catsharks

(especially *Scyliorhinus* in the eastern Atlantic), houndsharks (Triakidae, especially *Galeorhinus*, *Hemitriakis*, *Mustelus*, and *Triakis*), weasel sharks, and especially requiem sharks and hammerheads.

The large hammerheads and requiem sharks are dangerous to swimmers and divers, and the requiem shark family may contribute the bulk of shark attack cases through its abundance in warm waters where most shark attacks occur. A few requiem sharks, primarily the bull shark, *Carcharhinus leucas*, enter freshwater rivers and lakes far from the sea.

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All photos by the author unless otherwise indicated.

References and Further Reading

- Baldridge, H. D. 1974. *Shark attack*, 263 pp. New York, N.Y.: Berkeley Publishing Corp.
- Bigelow, H. B., and W. C. Schroeder. 1948. Sharks, Chapter 3 in *Fishes of the Western North Atlantic*, No. 1, Part 1, pp. 59-576. Memoir, Sears Foundation for Marine Research.
- Budker, P., and P. J. Whitehead. 1971. *The life of sharks*, 222 pp. New York, N.Y.: Columbia University Press.
- Compagno, L. J. V. 1973. Interrelationships of living elasmobranchs. In *Interrelationships of Fishes*, ed. P. H. Greenwood, R. S. Miles, and C. Patterson. Supplement 1, *Zoological Journal of the Linnean Society of London*, vol. 53, pp. 15-61.
- . 1977. Phyletic relationships of living sharks and rays. In *recent advances in the biology of sharks*, ed. R. G. Northcutt. *American Zoologist*, Vol. 17, no. 2, pp. 303-322.
- Gilbert, P. W., ed. 1963. *Sharks and survival*, 578 pp. Boston, Mass.: D. C. Heath and Co.
- Gilbert, P. W., R. F. Mathewson, and D. P. Rall, eds. 1967. *Sharks, skates and rays*, 624 pp. Baltimore, Md.: Johns Hopkins Press.
- Hodgson, E. S., and R. F. Mathewson, eds. 1978. *Sensory biology of sharks, skates and rays*, 666 pp. Arlington, Va: Office of Naval Research, Department of the Navy.
- Kreuzer, R., and R. Ahmed. 1978. Shark utilization and marketing, 180 pp. Rome, Italy: Food and Agriculture Organization of the United Nations.
- Lineaweaver, T. H., III, and R. H. Backus. 1969. *The natural history of sharks*, 256 pp. Philadelphia, Penn. and New York, N.Y.: J. B. Lippincott Co.
- Northcutt, R. G., ed. 1977. Recent advances in the biology of sharks, pp. 287-515. *American Zoologist*, vol. 17, no. 2.

Vision in Sharks

by Joel L. Cohen



Photo by
Chuck Davis

*The eyes were sightless in the black,
and the other senses transmitted
nothing extraordinary to the small,
primitive brain.*

Jaws, Peter Benchley

Such is the impression in popular literature regarding the vision of sharks. Thought to see poorly and only at night, sharks have even been called "swimming noses." Stories abound concerning sharks that home in on minute quantities of blood in the water from miles away, yet the animals' visual abilities are, for the most part, ignored. Where did these impressions about the poor visual system of sharks come from? How well do sharks see?

Most of the early research on sharks was done in the late 1800s and early 1900s by European anatomists. The specimens studied were those obtained from local fishermen. Knowledge of the shark visual system thus came from only two or

three species and was applied to all species. Hence, a "typical shark eye" was described, and was thought to be valid for all sharks. However, there are more than 300 species of sharks. They live in many different habitats, ranging from near shore to the deep sea. As we shall see, their visual systems adapt quite well to their specific environments.

Differences in Design of Eyes

The design of the shark eye closely follows that of the typical terrestrial vertebrate eye. But there are some notable exceptions. If one compares a cross section of a shark eye with that of the eye from a terrestrial vertebrate, there is a striking difference in the size and shape of the lens (Figure 1a, 1b, 1c).

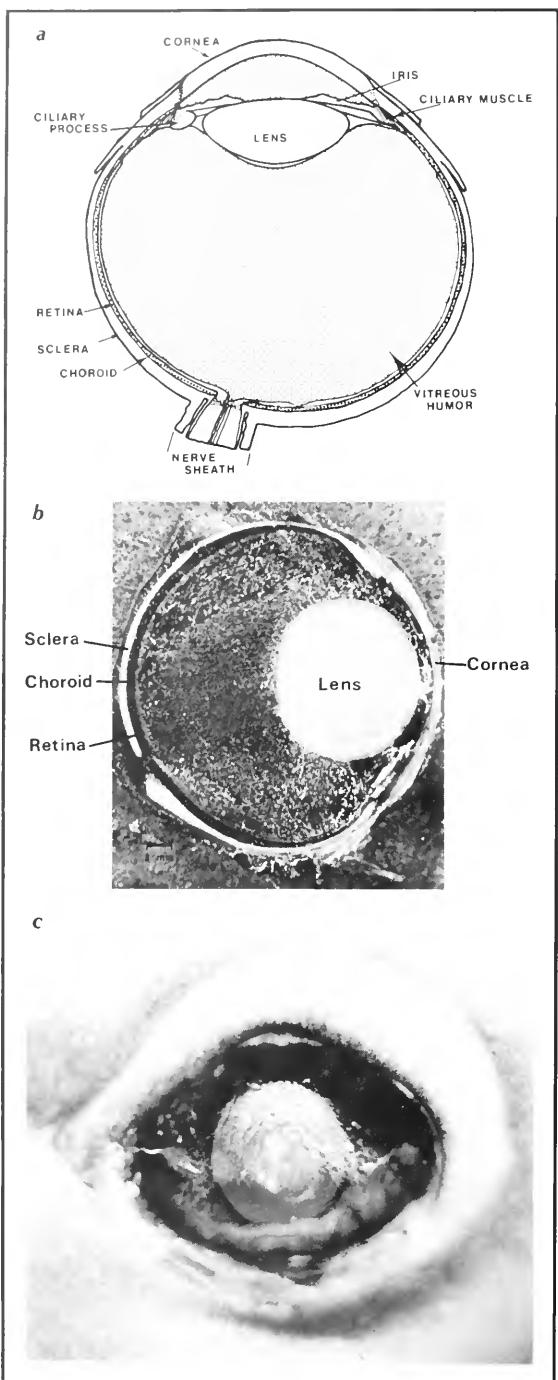


Figure 1. The vertebrate eye. a) Drawing of a typical terrestrial eye. The lens is thin and flattened. In relation to the rest of the eye, the lens takes up a proportionally small amount of space. b) Frozen section from the eye of a juvenile lemon shark, *Negaprion brevirostris*. The lens is large and almost spherical in shape. (Photo by R. E. Hueter) c) Photograph through the front of the eye of a six-gill shark, *Hexanchus griseus*. Note the large spherical lens.

Why is the lens of the shark so large and almost spherical in shape, while that of the terrestrial eye is small and flattened?

The cornea is the transparent front of the eye. In the terrestrial environment, there is a large difference between the density of the air and that of the cornea, the cornea being denser. This difference in density causes light rays entering the eye to be bent, or refracted. Because this refraction aids the lens in focusing the light on the photoreceptor cells of the retina, the lens does not have to be very powerful. As a result, eyes in land vertebrates have thin lenses that can change their point of focus by changing shape. This is accomplished by two small ciliary muscles.

In aquatic animals, however, the water and the cornea are of the same density, so the cornea cannot contribute to the focusing of an image. That job falls to the lens, which must be powerful. Hence, it is large, it can not accommodate or focus the image by changing its shape as the lenses in terrestrial vertebrates do. In teleosts (bony fishes), focusing is accomplished by means of the *retractor lensis* muscle, which, instead of changing the shape of the lens, moves the entire lens toward the retina. In sharks, the story is not yet clear. When electrodes are placed on the muscles attached to the lens, there is no noticeable lens movement. However, a difference in the focal point has been found between anesthetized and unanesthetized sharks, implying lens movement of some sort.

If the lens of a shark does not move, what is the quality of an image falling on the retina? This may determine the resolving power of the visual system. If a poor, unfocused image is projected onto the retina, then this would set a lower limit on how well the shark sees. In essence, it would be the weak link in the chain of the visual system.

Robert Hueter, now at the University of Florida, has examined the eyes of live juvenile lemon sharks much the same way an eye doctor examines human eyes. By constructing a mathematical model from frozen sections of eyes, Hueter has shown that the eyes of these young sharks are hypermetropic, or farsighted, by 2.76 diopters.* It is as if the lens were not powerful enough to focus an image onto the retina. In human terms, this is a moderate farsightedness; the person would need glasses for reading, but the condition would not be debilitating. Further research is needed in this area to determine if a mechanism exists to bring the eye into a condition of perfect focus.

In a number of species of skates and rays, an unusual focusing mechanism — termed a "ramp retina" — has been described by Dr. Jake Sivak of

*A diopter is a unit of measurement for lens power equal to the reciprocal of the lens focal length in meters.

the University of Waterloo, Ontario, Canada. This is a static mechanism consisting of a variation in the distance between the lens and retina. To focus on an image, the animal would only have to move the eyes or bend the head.

No matter what the quality of the shark's optical system, the aquatic environment in which the animal lives plays a vital role in what it sees and how well it sees. We are used to seeing through a medium that is for the most part clear. The underwater world is completely different. It is filled with particulate matter and tiny organisms that act to scatter light and degrade the quality of an optical image. And as one goes deeper, the spectral quality of light changes.

Rods and Cones

The actual process of vision takes place in the retina, a semi-transparent tissue located at the back of the eye. Embryologically, the retina is an extension of the brain. Five types of cells are found within the retina, and they are organized into three cellular layers and two plexiform or synaptic layers (Figure 2).

The first event of vision occurs when a photon of light strikes visual pigment in the photoreceptor cells. Photoreceptors occur as two types: rods and cones (Figures 3 and 4). Anatomists in the 1800s observed that animals which were active during daylight hours had retinas that contained a majority of cone photoreceptors, while rods predominated in the retinas of nocturnal animals. This led to the duplexity theory of vision, which correlated the activity patterns of an animal with the complement of photoreceptors in its retina. The theory also ascribed certain functions to each photoreceptor type. Rods were said to be used for nighttime or low-light-level vision as well as for achromatic vision. On the other hand, cones were functional during daytime and were responsible for chromatic, or color, vision.

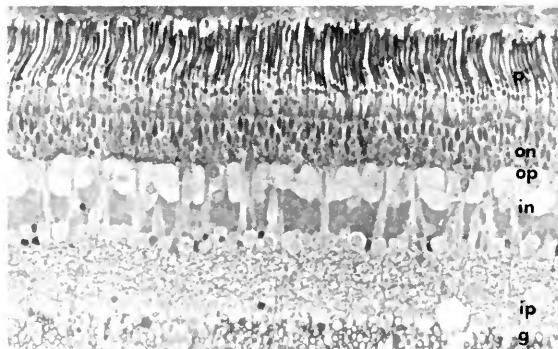


Figure 2. Light micrograph of the retina of the lemon shark. *p* = photoreceptors, *on* = outer nuclear layer, *op* = outer plexiform layer, *in* = inner nuclear layer, *ip* = inner plexiform layer, *g* = ganglion cell layer.

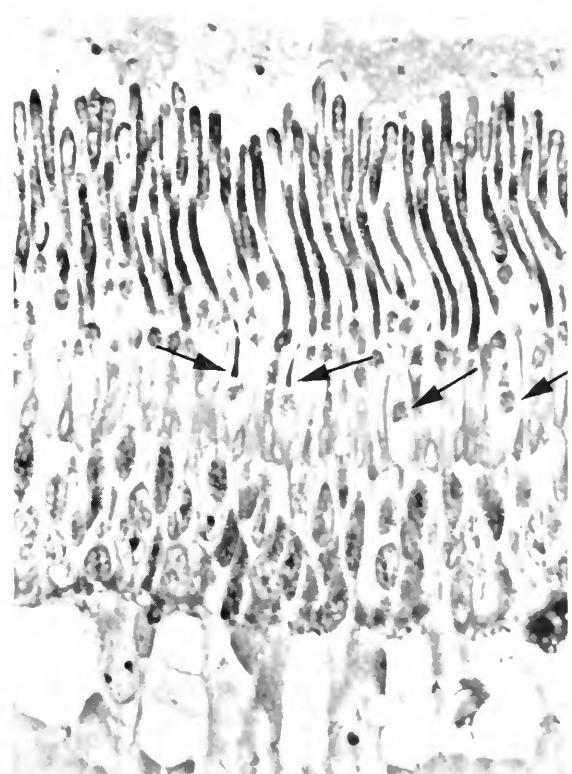


Figure 3. Light micrograph of the photoreceptor layer of the retina of the lemon shark. The arrows point to the cone photoreceptors. They have short, conically tapering outer segments. The remaining receptors are termed rod photoreceptors and have elongated cylindrical outer segments.

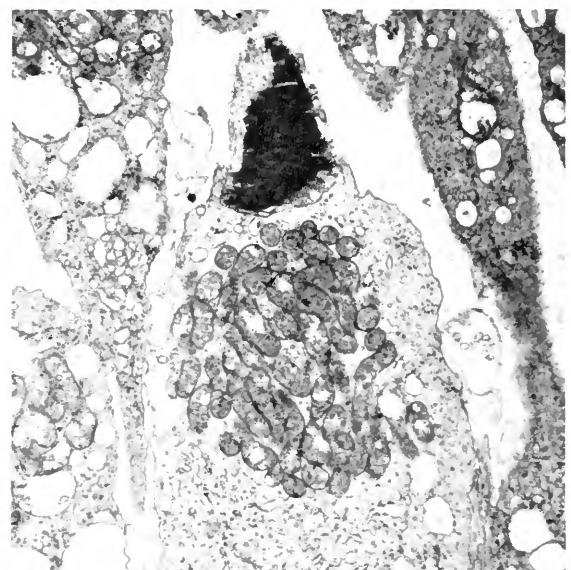


Figure 4. Electron micrograph of a cone photoreceptor from the retina of the lemon shark.

Because retinas from only a limited number of species were examined, sharks were categorized as possessing either rod or rod-dominated retinas. With the advent of better fixation techniques and better optics, the situation has changed.

The electron microscope has enabled scientists to divide photoreceptors into rods and cones based not only on their external morphology, but on ultrastructural criteria, such as whether the plasma membrane is continuous (cones) or discontinuous (rods) and whether the synaptic terminal is small and rounded (termed a spherule—rods) or larger and elongated (termed a pedicle—cones).

For example, the retina of the common dogfish, *Squalus acanthias*, was first studied by Retzius in 1896. Based on his observations and those of Verrier and Franz in the early 1930s, the retina was said to contain only rods. But in 1972, working with an electron microscope, Dr. William Stell showed that there also are cone photoreceptors present. Dr. Stell is now at the University of Calgary, Alberta, Canada.

In fact, most sharks possess duplex retinas, containing both rods and cones. Of all the elasmobranchs studied, the only exceptions to this are the skates *Raja erinacea* and *R. oscillata*, and possibly some of the deep-sea sharks.

What this means is that sharks are capable of both nocturnal and daylight activity. Possession of two types of photoreceptors also means that sharks might possess color vision. For this to occur, the spectral sensitivity of the two receptors must be different. Work done by myself and Dr. Samuel H. Gruber of the University of Miami have shown by electrophysiological methods that in the juvenile lemon shark at least two different spectral mechanisms are present and working together. Ultimate determination of color vision, however, rests with behavioral testing.

Green Light, Blue Light

In cross section, the outer segment of each photoreceptor consists of a series of stacked discs called lamellae (Figure 5). It is thought that the photopigment is located on or within the membrane of the lamellae. The rod visual pigment of sharks is based on vitamin A and is termed rhodopsin. It absorbs light maximally in the green part of the spectrum at approximately 500 nanometers.

Oceanic waters transmit the most light at approximately 500 nanometers. Thus the visual pigment of sharks is well matched to the environment. But there are species of sharks and skates that spend their entire lives in the deep ocean. As one goes deeper, the spectral quality of light changes, until only blue light is left.

Elasmobranchs having visual pigment with a maximum absorbancy in the green part of the

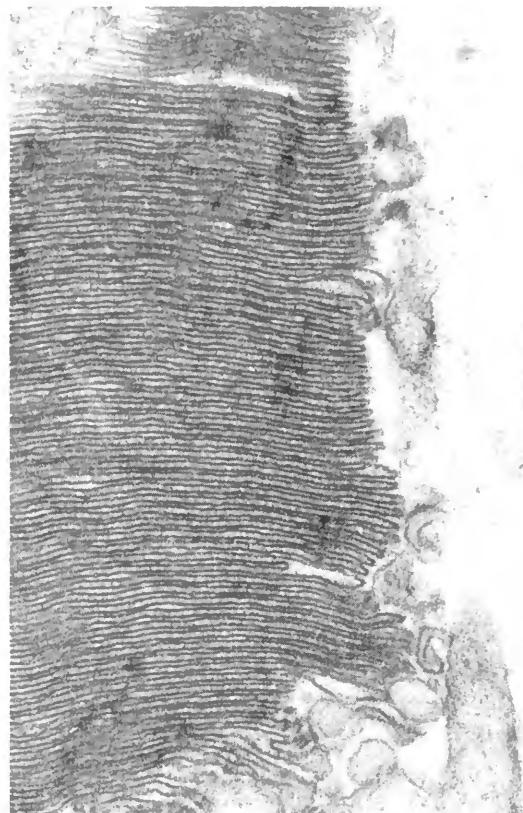


Figure 5. Electron micrograph of the outer segment of a photoreceptor showing the lamellae. The visual pigment is located on or within the lamellae membrane.

spectrum would be poorly adapted for life in the deep sea, where blue light predominates. However, deep-water sharks have been found to possess a golden visual pigment termed chrysopsin, which has its maximal absorbancy shifted 20 to 30 nanometers into the blue end of the spectrum, at 470 to 480 nanometers. So it appears that the elasmobranchs inhabiting the deep sea also have well-adapted visual pigments.

To make use of all the available light in the sea, elasmobranchs, like many vertebrates, possess a specialized ocular structure termed the tapetum lucidum. The tapetum is responsible for the eyeshine commonly seen in animals at night. The tapetum consists of a series of reflecting plates in the choroidal layer behind the retina (Figure 6). These plates are aligned differently in different parts of the eye so as to reflect entering light straight back along the same optical path. Thus, when a photon of light enters the eye and strikes a photoreceptor, it is reflected by the tapetum and strikes the photoreceptor a second time. This serves to increase the sensitivity of the eye.



Figure 6. Light micrograph of the retina of the lemon shark. The tapetal plates can be seen oriented at an angle so as to reflect light back onto the photoreceptor cells. CH = choroid layer, TP = tapetum lucidum, P = photoreceptors.

To protect the retina from too much light during the day, pigment granules migrate over the tapetum, thus blocking it from light. This occlusive tapetum is found in those sharks inhabiting pelagic waters. Deep-sea sharks, however, do not possess these screening pigment granules; their tapetums are always exposed to light.

Brain Studies

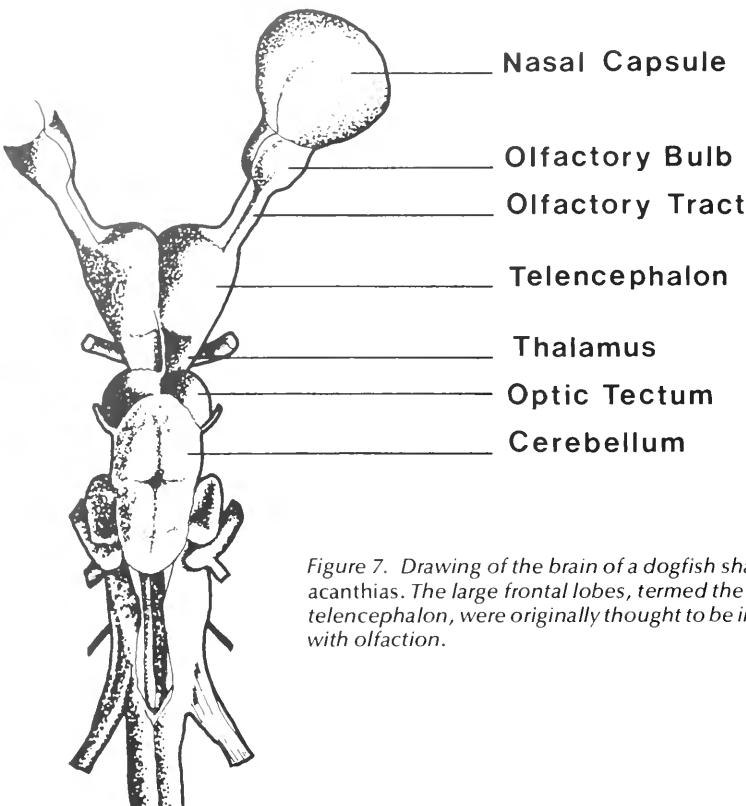
The orderly arrangement of cells in the retina serves to transfer and process the visual signals from the photoreceptors vertically via bipolar cells and laterally via horizontal cells and amacrine cells. The ganglion cells serve as the final relay station in the retina. Their axons form the optic nerve, through which visual signals are sent to the brain.

Unlike higher vertebrates, sharks do not possess a visual cortex. It has been thought that all

higher-center visual processing was done in the optic tectum of the brain (Figure 7), but new evidence suggests that the optic tectum is not as important in visual processing as once believed. In addition, other areas of the brain may play an important part in the processing of visual information.

This new information comes in part from anatomical and behavioral research done by Dr. Curt Graeber at Lerner Marine Laboratory, Bimini, the Bahamas. Graeber has shown that there is little difference in visually guided behavior between a nurse shark that has had its optic tectum surgically removed and one that has not. This is contrary to the findings of early scientists, who believed such an operation left the shark blind.

The belief that sharks were "swimming noses" came in part from the fact that the large area



*Figure 7. Drawing of the brain of a dogfish shark, *Squalus acanthias*. The large frontal lobes, termed the telencephalon, were originally thought to be involved only with olfaction.*

of the brain termed the telencephalon, or forebrain, was thought to receive only olfactory input. Dr. Sven Ebbesson of Catholic University in Ponce, Puerto Rico, and others, using the newer anatomical techniques that allow one to trace neural pathways, has shown that in the lemon, nurse, and tiger sharks, the telencephalon receives a large visual input from the optic tectum via the thalamus, a mid-brain structure. Further support for this comes from the recording of evoked electrical responses from the telencephalon when the optic nerve is electrically stimulated. Upon removal of all or part of the telencephalon, defects were found in visually guided behavior.

In conclusion, we have determined that the visual system of sharks is not as deficient as previously thought. In contrast to that depicted in the early literature, the visual system of sharks is highly developed. Sharks are more than "swimming noses," but they do not need a fine-detail visual system such as ours because their world is far different from ours. They require mechanisms that enable them to hunt prey, and, for this function, they are well adapted.

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Acknowledgments

I would like to thank Robert E. Hueter for permission to use material from his research as well as for many hours of useful discussion. I would also like to thank Dr. S. H. Gruber for giving me the opportunity to learn about vision in sharks.

Selected Readings

- Cohen, J. L., S. H. Gruber, and D. I. Hamasaki. 1977. Spectral sensitivity and Purkinje shift in the retina of the lemon shark, *Negaprion brevirostris* (Poey). *Vision Research* 17: 787-92.
- Graeber, C. 1978. Behavioral studies correlated with central nervous system integration of vision in sharks. In *Sensory Biology of Sharks, Skates and Rays*, ed. by E. S. Hodgson and R. F. Mathewson. Washington, D. C.: U. S. Government Printing Office.
- Gruber, S. H. 1975. Duplex vision in the elasmobranchs: histological, electrophysiological, and psychophysical evidence. In *Vision in fishes: new approaches to research*, ed. by M. A. Ali. New York: Plenum Press.
- Gruber, S. H., and J. L. Cohen. 1978. Visual system of the elasmobranchs: State of the art 1960-1975. In *Sensory Biology of Sharks, Skates and Rays*, ed. by E. S. Hodgson and R. F. Mathewson. Washington, D. C.: U. S. Government Printing Office.
- Gruber, S. H., R. L. Gulley, and J. Brandon. 1975. Duplex retina in seven elasmobranch species. *Bull. Mar. Sci.* 25: 353-58.
- Hueter, R. E., and S. H. Gruber. 1980. Retinoscopy of aquatic eyes. *Vision Res.* 20, 197-200.
- Sivak, J. G. 1978. Refraction and accommodation of the elasmobranch eye. In *Sensory Biology of Sharks, Skates and Rays*, ed. by E. S. Hodgson and R. F. Mathewson. Washington, D. C.: U. S. Government Printing Office.



Figure 1. The "looseness" of the upper jaw of a mako shark, *Isurus oxyrinchus*, is demonstrated. By protruding the upper jaw during the bite, many sharks are able to gouge chunks out of large prey. (Photo by Marty Snyderman)

Shark Feeding Mechanisms

by Sanford A. Moss

A key to individual survival and evolutionary success is adequate nutrition. A reasonably full belly is necessary in order to grow, move, mature, and mate. Feeding mechanisms, along with their concomitant locomotor and sensory gear, are critical features in any animal's existence. The evolutionary persistence of sharks can in some measure be explained by their success in feeding. This comes as no surprise to a public that is educated to the view that sharks eat spectacularly, successfully, and often gruesomely. Moreover, the public—and many scientists—think of sharks as primitive beasts that have persisted in the modern world only as prehistoric anachronisms. Such thinking is fallacious: sharks are elegantly adapted animals, and their feeding mechanisms are apt examples of their economy of form and function.

Sharks are particularly well equipped in the sensory aspects of feeding, as consideration of their

olfactory, electrosensory, visual, and acousticolateralis systems suggests. They also seem particularly able to avoid detection by potential prey. Scientists have been surprised at finding fast swimming tuna and billfish in the stomachs of apparently lethargic sharks, such as the oceanic whitetip, *Carcharhinus longimanus*. Sharks make very little hydrodynamic noise when swimming, and may thereby escape acoustic detection by prey (see *Oceanus*, Vol. 23, No. 3). Also, the color patterns of many sharks are probably very cryptic in their feeding environments, making them functionally invisible to the prey they seek. Our understanding of these matters is sketchy, however, and more work needs to be done on this aspect of their feeding success.

The actual ingestion of prey by sharks is accomplished with an anatomical system that is elegant in its simplicity and effectiveness. With

relatively small modifications of the basic feeding mechanism, elasmobranchs have evolved into a surprising number of functional types, feeding on different foods.

The feeding mechanism of typical carcharhiniform sharks has a characteristic external appearance (Figures 1 and 2). The mouth is tucked well behind the snout on the underside of the head, giving the animal its peculiar "chinless" appearance. The mouth is broad, but not long. It has numerous sharp teeth which, in most species, are not evident until the animal opens its mouth wide (Figure 2). The shortness and ventral position of the mouth may seem awkward for a top predator. Predaceous bony fishes, such as barracudas and pikes, have long jaws at the fronts of their snouts. Moreover, these fishes can see their own mouths and thus "look" food into them; sharks cannot. These seeming disadvantages, however, are not consequential. Sharks can eat anything a barracuda can—and more.

Three Important Features

The internal anatomy of the shark feeding mechanism has three important features: the skeletal elements, including the braincase (chondrocranium) and the jaws; the cranial musculature which moves the skeletal elements; and the teeth.

Sharks lack true bone in the skeletal system. The basic skeletal material in these animals is cartilage, which is flexible, but does not resist

mechanical deformation well. Where hardness becomes necessary in cartilage, sharks have strengthened it by the deposition of calcium salts in the surface layers of the skeletal element. The jaws and chondrocrania of sharks are thus often hardened by these calcium salts. Indeed, it is sometimes possible to make inferences about the diets of various shark species by examining the degree to which their jaws are calcified. For example, nurse sharks, *Ginglymostoma cirratum*, which feed predominantly on hard-shelled molluscs and crustaceans, have significantly heavier jaws than fish-eating sharks.

The jaws of carcharhinoid sharks (Figure 3) typically consist of tooth-bearing upper (palatoquadrate cartilage) and lower elements (mandible or Meckel's cartilage). They are formed from paired cartilages that meet in symphyses (joints) at the midline in the front of each jaw. These connections are loose, allowing each side of the jaw a fair amount of latitude in its movement. Sharks that eat tough prey, such as tiger sharks, may have tight, well-fused symphyses. The jaw cartilages are expanded toward the rear, allowing large attachment surfaces for the considerable muscle masses that close the jaws. The upper and lower jaws meet in a special joint, which allows vertical flexibility but resists lateral movement. This articulation really consists of two ball-and-socket joints, arranged next to each other with one ball from the upper jaw fitting into a mandibular socket and the other ball from the mandible fitting into a palatoquadrate socket.

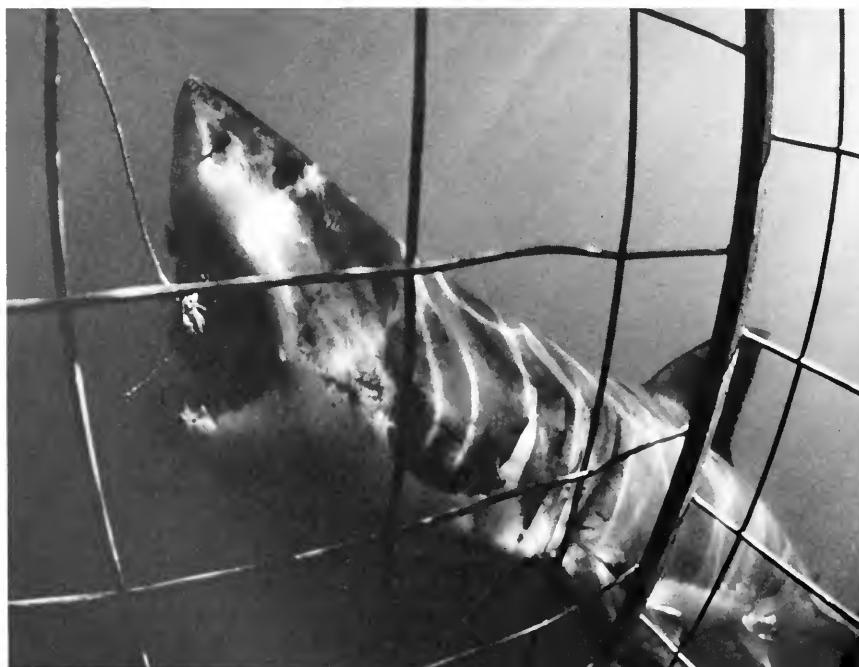


Figure 2. A great white shark, *Carcharodon carcharias*, attacking bait suspended next to a shark cage in Australian waters. The ventrally placed mouth is broad, but relatively short. Sharks evolved a more powerful biting apparatus by reducing the length of the jaws. (Photo by David Doubilet)

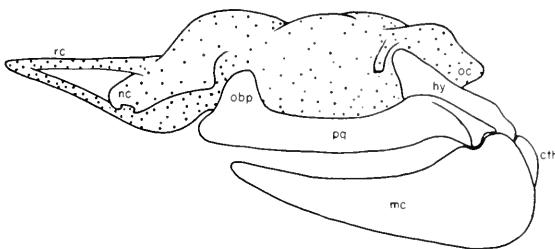


Figure 3. Lateral view of a carcharhinid shark chondrocranium (stippled) and jaw complex. The upper and lower jaw are loosely connected to the chondrocranium by the hyomandibular cartilage and by the ethmopalatine ligament (not visible here), which runs from the orbital process of the upper jaw to the underside of the chondrocranium. *cth*—ceratohyal cartilage; *hy*—hyomandibula; *mc*—Meckel's cartilage; *nc*—nasal capsule; *obp*—orbital process; *oc*—occiput; *pq*—palatoquadrate cartilage; *rc*—rostral cartilage. (From Moss, 1972).

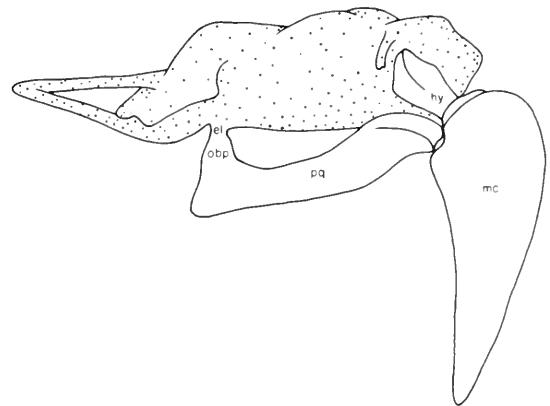


Figure 4. Lateral view of a carcharhinid shark chondrocranium (stippled) and jaw complex with the jaws maximally opened and the upper jaw protruded. The outer end of the hyomandibula has been pulled forward and laterally, bracing the jaws. The palatoquadrate cartilage has been pulled down to the limit imposed by the ethmopalatine ligament. The upper jaw teeth can thus cut deeply into the prey. *el*—ethmopalatine ligament; *hy*—hyomandibula; *mc*—Meckel's cartilage; *obp*—orbital process (From Moss, 1972).

The jaws are loosely connected to the rest of the skull at two points. First, a ligamentous connection runs from knobs (orbital processes) near the front of each side of the upper jaw to the underside of the chondrocranium (Figure 4). With the jaws closed, these ligaments (ethmopalatine ligaments) are slack and have no suspensory function. When the jaws are engaged in biting, however, these ligaments passively restrain the upper jaw from making excessive downward movements. They are in a sense "safety lines."

The second and principal connection of the jaw complex to the chondrocranium is by cartilages, the hyomandibulae. These cartilages serve as struts or braces that run on each side from the lateral posterior (otic) surface of the chondrocranium back to the inner surface of the rear-most portion of the lower jaw, near its articulation with the upper jaw. The connections made here are also loose, allowing the ends of the hyomandibulae to swing out and forward, pushing the rear ends of the jaws outward and, in some sharks, pushing the entire jaw complex forward as well (Figure 4).

When the jaw apparatus of a shark is carefully dissected, it is easy to appreciate a similarity in the form and position of the jaws and hyomandibulae with the rows of cartilages behind them, supporting the gill apparatus. In fact, it has long been a tenet of comparative vertebrate anatomy that the jaws represent a modification of the first in a series of ancestral gill or branchial arches. According to this idea, the hyomandibula is a modification of part of the second in this series of primitive gill arches. In some living sharks, such as the six-gill shark, *Hexanchus griseus*, this second, or hyoid, arch actually supports functional gills.

Many living sharks, as well as skates and rays, also have openings behind the eyes known as

spiracles. These openings into the pharynx are remnants of the gill slit between the mandibular and hyoid arches. In addition to the hyomandibula, additional cartilages exist in the hyoid arch. The ceratohyal cartilages pass down and forward from articulation points at the ends of the hyomandibulae to meet the lower jaw. These ceratohyal cartilages curve just inside the mandibles to articulate with a single, median basihyal cartilage. Together with other gill-arch cartilages projecting forward in the bottom of the mouth, these elements form a "tongue," which is pulled down and back to enlarge the oral cavity during feeding and ventilation.

The Muscles of the Jaw

The muscles that operate the jaw complex are large and conspicuous. The most obvious group, the first met in a lateral dissection, is the quadrato-mandibularis complex (Figure 5). It runs from the posterior expanded portion of the palatoquadrate down to the lower jaw. This large muscle mass is divided into smaller muscle groups in different species, but its major function is to close the jaws by pulling them together.

Three other large muscles also participate in the generalized shark feeding apparatus. These include levators of the hyomandibulae and upper jaws (levator hyoideus and levator palatoquadrati, respectively). These two muscles run from attachments high on the chondrocranium to the rear ends of the hyomandibula and upper jaw

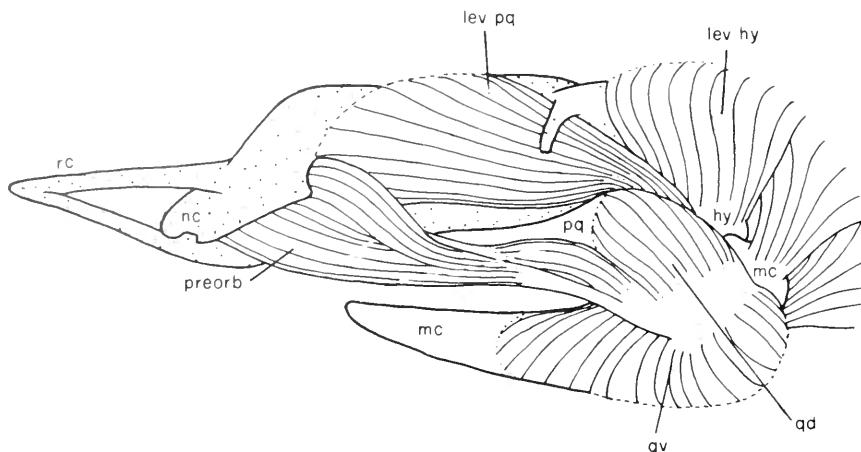


Figure 5. Musculature of the carcharhinid feeding mechanism. The jaws are closed principally by the quadratomandibularis complex (qd and qv) with help from the preorbitalis muscle (pre orb). The levator palatoquadratii (lev pq) and preorbitalis pull the jaw complex forward, helping to protrude the upper jaw. The levator hyoideus (lev hy) raises the hyomandibula and pulls it forward, bracing it between the chondrocranium and the jaw complex, thus supporting the apparatus against the lateral forces generated during feeding. hy—hyomandibula; mc—Meckel's cartilage; pq—palatoquadrate. (From Moss, 1972).

(Figure 5). The third muscle, the preorbitalis, also originates well forward and high on the chondrocranium and runs down and back to join the quadratomandibularis, where it attaches to the lower jaw. The effect of these three muscles is similar in carcharhiniform sharks. Together they pull the back of the jaw complex forward, rotating it so that the front of the upper jaw is forced forward and down. The outer ends of the hyomandibulae are also pulled laterally, pushing the articulation point of the jaws outward and effectively bracing the sides of the jaws against the tough skin of the head. The hitherto loose jaw complex is now stiffened, able to withstand the side-to-side forces generated during feeding.

The quadratomandibularis and the jaws act as a third-class lever system with the force (muscle) acting between the fulcrum (jaw articulation) and the resistance (food). For maximum power to be exerted, the moment arm (length of jaw) should be as short as possible. Sharks have very powerful biting capabilities.

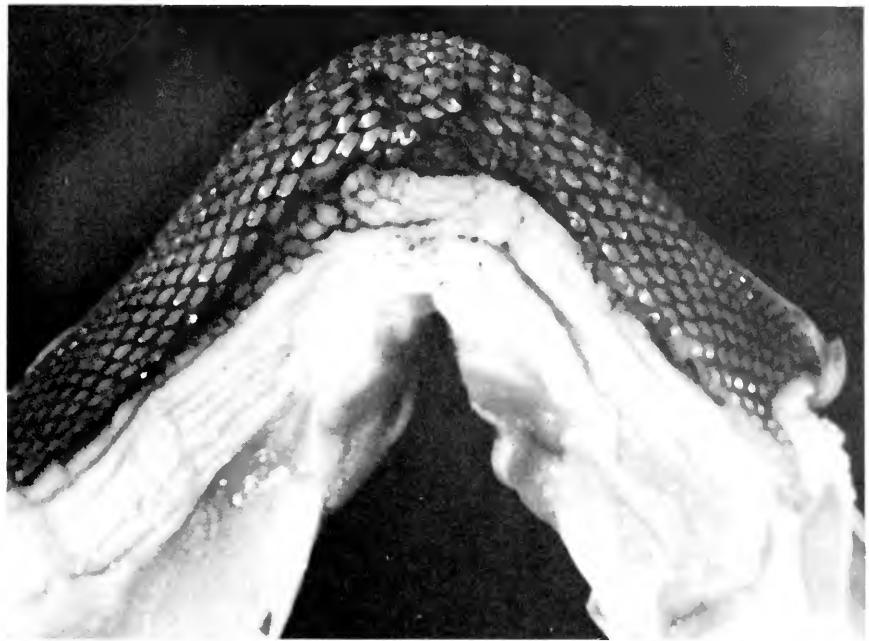
The effects of the levator and preorbitalis muscles are considerable in shark feeding. They produce an effective upper-jaw protraction mechanism that allows the upper jaw to take an active role in feeding (Figure 2). The upper jaw during protraction can thus bite deeply into the kerf made by its sharp teeth. Most predators that live on fishes are limited to prey which they can engulf at a single bite—hence the long jaws of the barracuda and pike. Carcharhiniform sharks, however, are able to gouge chunks out of prey that are too large to be

taken into the mouth in one bite. This opens up new gastronomic worlds to the shark, placing large teleosts, whales, and even other sharks on their menu.

A Rapid Turnover of Teeth

One of the many unique characteristics of living elasmobranchs is a dentition that appears to be continually replaced throughout their lifetimes (Figure 6). As early as 1846, Sir Richard Owen—an anti-evolutionist who was to be a thorn in Charles Darwin's side—called attention to the elasmobranch dental array, calling it a "phalanx . . . ever marching slowly forward in rotatory progress over the alveolar border of the jaw." Subsequent to Owen's description, controversy arose as to whether sharks really do replace their teeth. In 1948, James Ifft and Donald Zinn, working in Woods Hole, demonstrated that the smooth dogfish, *Mustelus canis*, replaced its teeth at a rate of one functional row of teeth every 10 to 12 days. In 1967, I marked the teeth of young, captive lemon sharks, and recorded replacement rates of about one functional row of teeth a week. Similar tooth replacement times have since been measured in other species of sharks. What is the reason for such a rapid turnover of teeth?

Shark teeth are relatively fragile. In the face of the biting force sharks routinely produce, it is not surprising to find that these teeth are often broken (Figure 6). Rapid replacement of teeth thus allows sharks to compensate for the premature disintegration of their dentition—an adaptation that



*Figure 6. The lower jaw of the smooth dogfish, *Mustelus canis*, as seen from above. In this species the teeth are low and rounded, producing a modified crushing dentition. Several generations of teeth are functional at any one time. The replacement of teeth occurs by an outward movement (toward the top of the picture). The younger, replacement teeth at the bottom can be seen to be slightly larger than the older, outer teeth, thus compensating for growth of the shark. It is not unusual to find shark dentitions, like this one, with damaged teeth. (From S. A. Moss, 1972, Tooth replacement and body growth rates in the smooth dogfish, *Mustelus canis* [Mitchell]. Copeia, 1972 (4): 808-811).*

befits the predatory lives they lead. Tooth replacement also allows for growth. As the shark grows, so does its jaws. The number of teeth, however, remains constant. Each tooth family (the replacement teeth in a single sequence) must grow in order to maintain a set of teeth large enough to carry out the requisite predatory tasks. Each tooth is thus a little larger than the one it replaces.

Most sharks have a heterodont dentition. This means that all the teeth are not morphologically the same. Carcarhiniform sharks, for instance, often have broader teeth in the upper jaw than in the lower. In some sharks (a good example being *Heterodontus francisci*, the horned shark), the dentition in a single jaw may vary considerably from sharp, cutting teeth in the front of the jaw to crushing, molar-like teeth in the back. Some of these differences in tooth structure become meaningful when the diet and feeding behavior of each species of shark is considered (Figure 7).

Feeding Behavior

Contrary to what is often written about sharks, there is not a lot of unpredictable behavior associated with their feeding. Once a decision is made to

attack, that decision is communicated to the observer clearly. Carcarhiniform sharks may slowly circle a prospective prey, and even bump it tentatively with the snout or pectoral fins. When the decision is made to attack, however, this behavior is altered dramatically. The shark is transformed from a sinuously swimming, graceful creature to a stiffened, herky-jerky animal. The back may seem arched, the body is stiff, and the tail beats more quickly. The shark will now swim directly at its intended victim with its snout somewhat elevated. The jaws may be opened and closed rapidly—as often as three times per second—during this closing rush. As the shark approaches its prey, the pectoral fins are depressed, raising the forepart of the body and braking the animal's speed. The opened mouth makes contact with the prey and, as soon as the teeth obtain a purchase, the shark begins to shake its head and forebody from side to side. The frequency of head shaking varies from species to species. Tiger sharks rather slowly throw their massive heads from side to side, while gray reef sharks, *Carcharhinus amblyrhynchos*, quickly shake their heads in what almost seems like a vibration. Whatever the species, the effect is the same. These side-to-side movements bring the

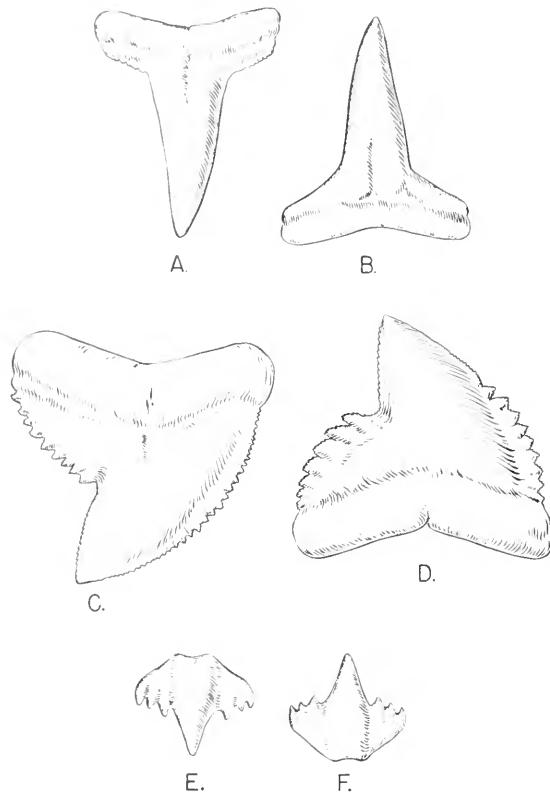


Figure 7. Three examples of some forms of shark teeth. A and B are the upper and lower jaw teeth, respectively, of the lemon shark (*Negaprion brevirostris*). In this species, which usually feeds on fish, the upper jaw teeth are not very much broader than those in the lower jaw. C and D represent teeth from the tiger shark (*Galeocerdo cuvieri*). These heavy, serrated teeth make effective saws for cutting through the sea turtles they frequently eat. E and F are teeth from the nurse shark (*Ginglymostoma cirratum*). The teeth in this species are relatively small and serve to hold prey, such as crustaceans that have been sucked into the mouth, while the heavy, broad jaws crush them.

sharp lateral cutting edges of the teeth into play, slicing ever deeper into the prey. The major role played by the upper jaw is reflected in the dentition of carcharhiniform sharks. Many species have broad, blade-like teeth confined to the upper jaw. The awl-like lower jaw teeth are designed for puncturing and holding the prey while the upper jaws do their work.

This feeding mechanism is capable of more versatility than merely taking bites out of large prey. Carcharhiniform sharks, to some extent, are dietary generalists. While the bulk of their diet may be fish and squid, most are not above eating benthic invertebrates, such as crabs, lobsters, and octopuses.

Certain species do seem to have preferences—hammerheads (*Sphyrna spp*) prefer sting rays; bull sharks (*Carcharhinus leucas*) often eat other sharks; smooth dogfish are crab and lobster specialists; and tiger sharks attack sea turtles with regularity. But all possess a feeding mechanism of great versatility that helps to make them perhaps the ultimate predatory type.

The carcharhiniform gouging mechanism is but one of a surprising number of feeding mechanisms evolved by sharks. The basic type is the crushing-feeding mechanism. This features heavy, short—almost transverse—jaws; short, heavy hyomandibulae incapable of much lateral or forward movement, and a heavy molariform dentition. This feeding mechanism is seen in rays and is admirably suited to ingesting and crushing hard-shelled benthic invertebrates, which are sucked into the small ventral mouth by considerable orobranchial expansion. Orbital processes are reduced or lacking on the upper jaws, for lateral head-shaking is not important. The Orectolobiformes, which include nurse and carpet sharks, have secondarily adopted this sucking and crushing feeding-mechanism.

Another distinctive feeding type is that shown by many squaliform dogfishes. These animals also tend to have short, transverse jaws with short hyomandibulae (Figure 8). The dentition, however, is composed of low, blade-like teeth which are often tightly overlapped into rows of very sharp cutting edges. The orbital processes are very long and project nearly to the top of the chondrocranium when the mouth is closed. In the absence of a long hyomandibula to brace the rotating jaws against the braincase, the orbital processes maintain contact with the braincase even during periods of extreme upper jaw protrusion. The resultant feeding mechanism is an effective cutting one, able to slice up herring-sized fish into smaller pieces. Some of these sharks—such as the deep-water, luminous shark, *Isistius brasiliensis*—are known to gouge chunks out of large prey.

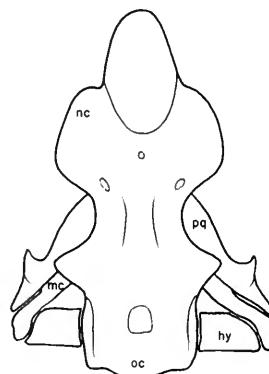


Figure 8. Dorsal view of the chondrocranium and jaw complex of the spiny dogfish, *Squalus acanthias*. The short, laterally directed hyomandibulae cannot be pulled further outward to brace the jaw complex. The orbital processes (not shown here) are very long and do not lose contact with the sides of the chondrocranium when the upper jaw is protruded. (From Moss, 1977).

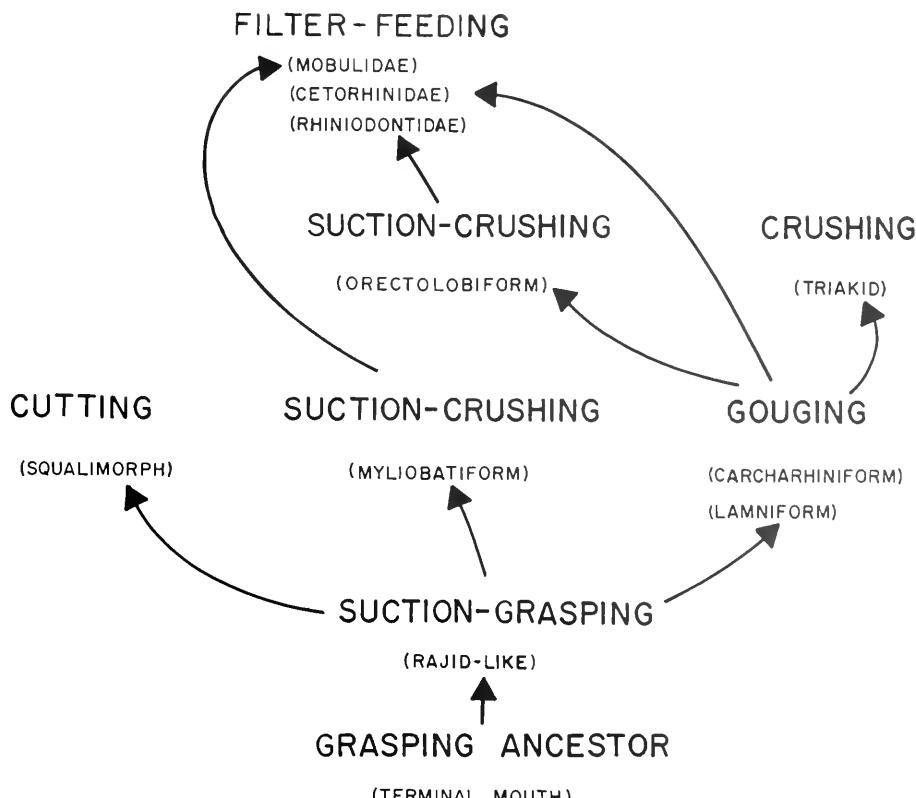


Figure 9. Possible evolution of feeding mechanisms in elasmobranchs. The ancestral type was probably not unlike that of modern teleosts, such as pikes. A small ventral mouth, similar to living skates, evolved to deal with small ventral invertebrates. This basic suction-grasping mechanism evolved into 1) a cutting-feeding mechanism seen in living dogfishes; 2) a crushing mechanism found in many living rays; and 3) with the advent of elongate hyomandibulae and sharp cutting teeth, into the gouging-feeding mechanism of living carcharhiniform and lamniform sharks. Further modifications produced a secondary crushing-feeding mechanism and, at least three times, the filter-feeding mechanism seen in living manta rays, whale sharks, and basking sharks. (From Moss, 1977).

Filter-Feeding Sharks

Perhaps one of the most spectacular evolutionary modifications of shark feeding mechanisms was the development of filter-feeding for planktonic organisms. This mechanism was developed by: 1) elongation and broadening of the jaws; 2) often moving the mouth forward to its ancestral location at the front of the snout; 3) reducing the dentition; and 4) increasing spectacularly the size and number of gill rakers in the pharynx to act as a filter. The evolution of filter-feeding has occurred at least three different times among elasmobranchs. It first happened in mobulid rays, such as *Manta birostris*, by modification of the primary crushing-feeding mechanism (Figure 9). Secondly, the whale shark, *Rhincodon typus*, resulted from modification of a secondary crushing-feeding mechanism seen today in its orectolobid (nurse shark) relatives. Finally, the gouging lamniform sharks—represented by such as the spectacular mako, *Isurus oxyrinchus*, and great white shark, *Carcharodon carcharias*—produced the filter-feeding basking shark, *Cetorhinus maximus*.

The evolution of sharks has been a rich and varied process. The diversity of feeding

mechanisms in living sharks is extraordinary in view of the relatively small number of extant species.

Sharks comprise a group of finely tuned predators, which in their diversity are well equipped to survive whatever environmental exigencies may lie ahead.

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Selected Readings

- Gilbert, P. W. 1962. The behavior of sharks. *Scientific American* 207(1): 60-68.
- Johnson, R. H., and D. R. Nelson. 1973. Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. *Copeia* 1973: 76-84.
- Moss, S. A. 1967. Tooth replacement in the lemon shark, *Negaprion brevirostris*. In *Sharks, Skates and Rays*, ed. P. W. Gillett, R. F. Mathewson, and D. P. Rall, pp. 319-329. Baltimore, Md.: The Johns Hopkins Press.
- . 1972. The feeding mechanism of sharks of the family Carcharhinidae. *J. Zool. (London)* 167: 423-436.
- . 1977. Feeding mechanisms in sharks. *Amer. Zool.* 17: 355-364.

Patterns of Shark Reproduction

by Perry W. Gilbert

One reason sharks have survived many millions of years is because of their reproductive capabilities. In all species, some 300 to 350 in number, semen is introduced into the female, fertilizing eggs at the upper end of her genital tract. Although most sharks produce relatively few young at one time, the embryos receive substantial protection, either inside resistant egg cases or within the body of the mother until birth. Once the young sharklet or "pup" is released from the egg or from the mother, it is on its own, for there is no parental care. At this critical time, it may be devoured by predators, including other sharks, but sufficient numbers survive to handily perpetuate the species.

Male Reproductive Structures

Claspers. The sex of any shark may be readily recognized, for the males possess prominent cylindrical extensions of their pelvic fins known as claspers. First reported by Aristotle, it was thought that these structures served to embrace and hold the female during the mating act. Actually, one of these claspers is introduced into the distal end of the oviduct of the female during copulation, and sperm pass from the male along a groove in the clasper into the reproductive tract of the female.

Claspers may be recognized even in small embryos but do not become conspicuously developed until the testes of the male begin to produce sperm. We have found in several species of sharks that the growth of the claspers is very rapid at about the time the testes begin to produce sperm (Figure 1), and in a matter of a few months the shark passes through a period analogous to puberty in man.

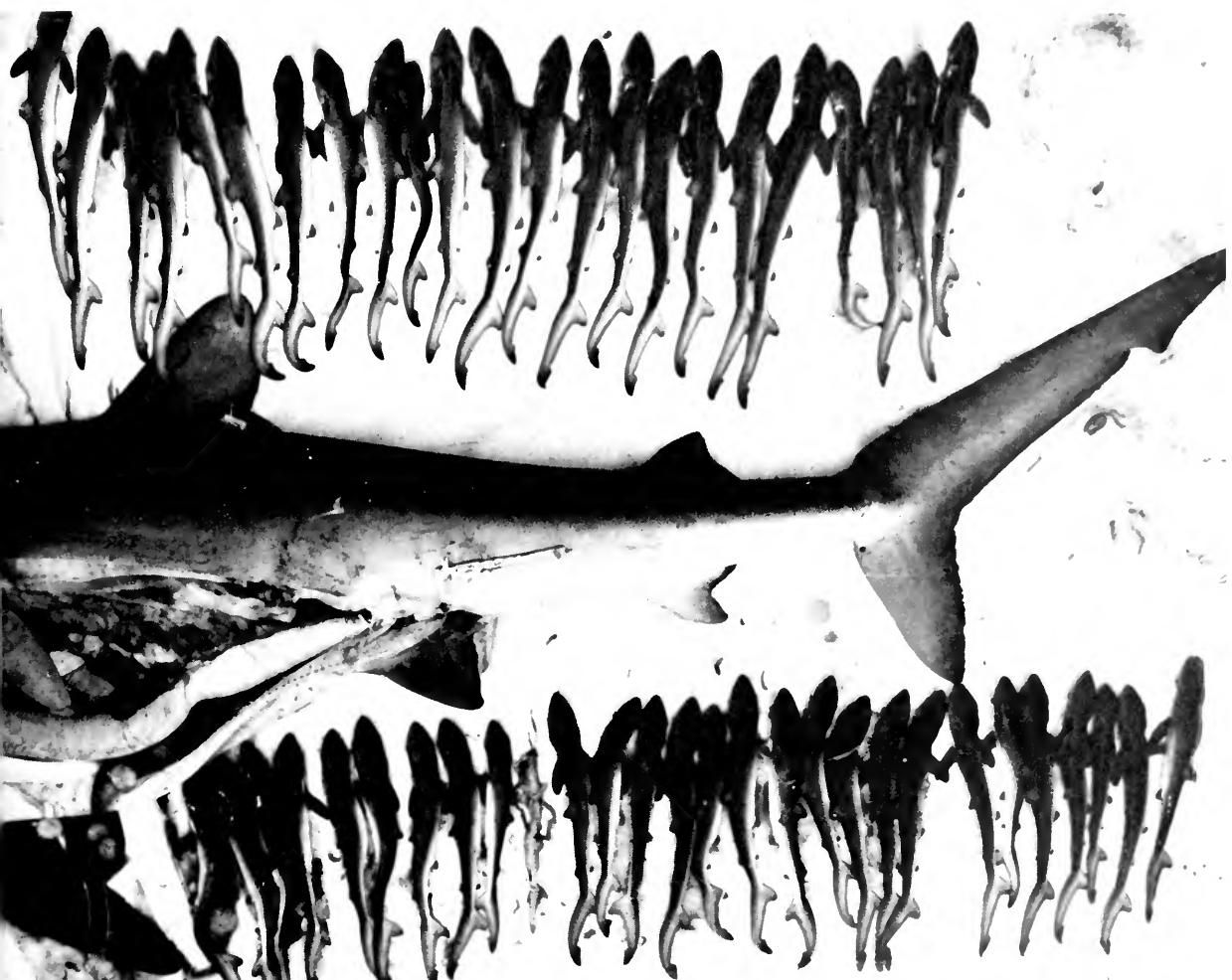
In all sharks, the claspers are supported by cartilaginous rods, frequently calcified, and in some, such as the spiny dogfish, *Squalus acanthias*, the distal end of each clasper possesses a prominent spine that is erected once the clasper is inserted, thus anchoring the male securely to the female. In the sandbar shark, *Carcharhinus milberti*, the tip of the clasper expands after insertion into the oviduct of the female; the cartilages of the tip open like the



ribs of a fan at right angles to the clasper axis. The expanded tip not only holds the oviduct open for the passage of sperm but also prevents withdrawal of the clasper.

Siphon sacs. Associated with each clasper is a curious muscular bladder that lies just beneath the belly skin of all sharks. These paired structures, known as clasper siphons (Figure 2), open distally into each clasper groove. According to W. Leigh-Sharpe (1920. *J. Morph.* 34: 245-65), the siphon sacs become filled with seawater prior to mating and, after the clasper is inserted, seawater is discharged from one of the sacs and washes sperm along the clasper groove into the body of the female.

The problem of how these empty clasper siphons became filled with seawater long puzzled us. It is just not possible to place an empty bladder, devoid of all air, in seawater and, by squeezing, fill it. The shark must in some way force or pump water into these sacs.

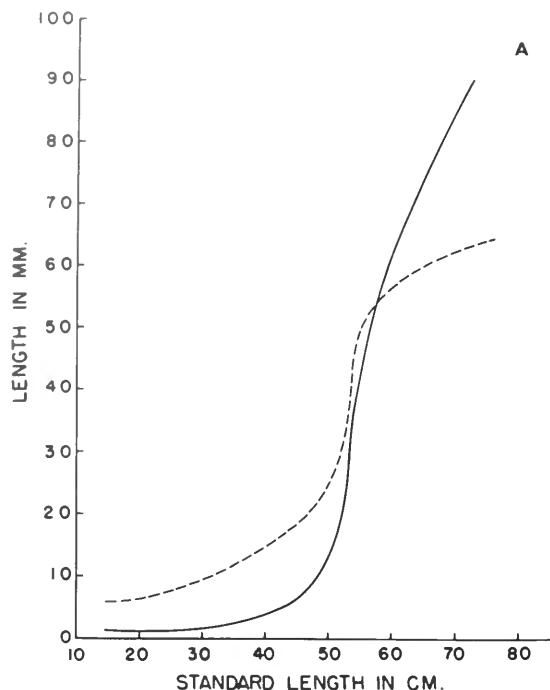


This 2.5-meter female blue shark, *Prionace glauca*, was carrying 52 sharklets when she was caught in a shark-fishing tournament off Long Island, New York. Tenth from left on the bottom row is a decomposing embryo that was already dead when its mother was disemboweled. (Photo by Harold Wes Pratt, National Marine Fisheries Service)

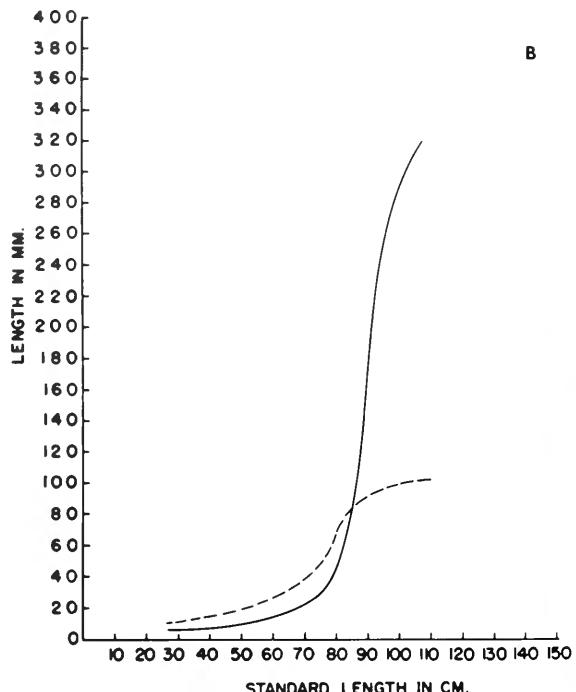
In 1958, while working at the Mt. Desert Island Biological Laboratory in Maine, I noticed on two occasions that adult male spiny dogfish periodically flexed their right or left clasper so that it formed a 90-degree angle with the long axis of their body (Figure 3). When I examined the siphons of these sharks, I found them partly filled with seawater. By manually flexing each clasper inward, when the shark was submerged, it was possible to pump additional seawater into the siphons. Each time the clasper was flexed, a fleshy funnel extended outward from the base of the clasper and served to direct water into the open distal end of the siphon. If the shark was moved forward through the water with the clasper tied in the flexed position, the funnel again served to divert water into the siphon associated with the flexed clasper. The spiny dogfish voluntarily flexed only one clasper at a time,

and in no case did it rotate its clasper inward more than 90 degrees.

It would appear, then, that the siphon may be filled as the shark moves through the water with clasper flexed. Some species may rest in one position and pump water into their siphons by alternately flexing and extending each clasper. In this regard, Stewart Springer injected an isotonic solution into the caudal vein of an adult male blacktip shark, *Carcharhinus limbatus*. He was able to induce the claspers to revolve inward and forward—the presumed mating position of the claspers for this species. In 1960, Springer stated: "As the claspers moved into a forward pointing position, a funnel, formed by a membrane supported by rods of cartilage, opened at the base of each clasper. The mouth of the funnel was also directed forward and the constricted end led into



A



B

Figure 1. Growth curve of clasper (broken line) and siphon sac (solid line) in (A) the spiny dogfish, *Squalus acanthias*, and (B) the smooth dogfish, *Mustelus canis*. (From Gilbert and Heath, 1972)

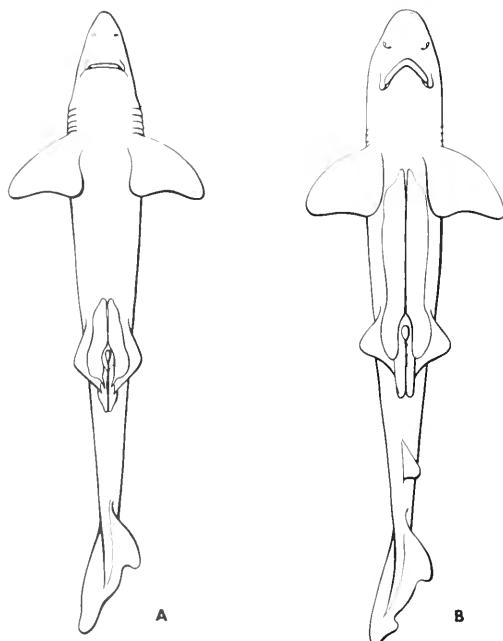


Figure 2. Siphon sacs of (A) the spiny dogfish and (B) the smooth dogfish, ventral aspect. The siphon sacs are situated between the belly skin and body musculature, end blindly at their forward end, and open into the clasper groove distally. (From Gilbert and Heath, 1972)

the siphon. The caudal vein was plugged experimentally to hold the claspers and funnel in position and the shark was moved forward as rapidly as possible through the water. This caused the clasper siphons to fill with water. Application of additional pressure to the caudal vein resulted in complete expansion of the fan-like tip of each clasper."

In addition to drawing in seawater prior to copulation, the clasper siphons are lined with epithelial cells that secrete a clear, sticky, slightly acid, mucus-like polysaccharide-protein substance. This substance serves to lubricate the clasper during copulation and may also contribute to the transport of seminal fluid and sperm (Gilbert and Heath, 1972).

Sperm formation and storage. The testes of sharks, in which the sperm are formed, are paired structures and are located at the forward end of the body cavity. They connect via several efferent ductules with the anterior portion of the elongate kidney on each side. Transformed kidney tubules convey the sperm from the efferent ductules to the *ductus deferens*. A modified portion of the anterior kidney, known as Leydig's gland, secretes seminal fluid into the *ductus deferens*. In some species, for example *Cetorhinus maximus* and *Prionace glauca*, sperm traveling along the *ductus deferens* are enclosed in packets known as spermatophores.

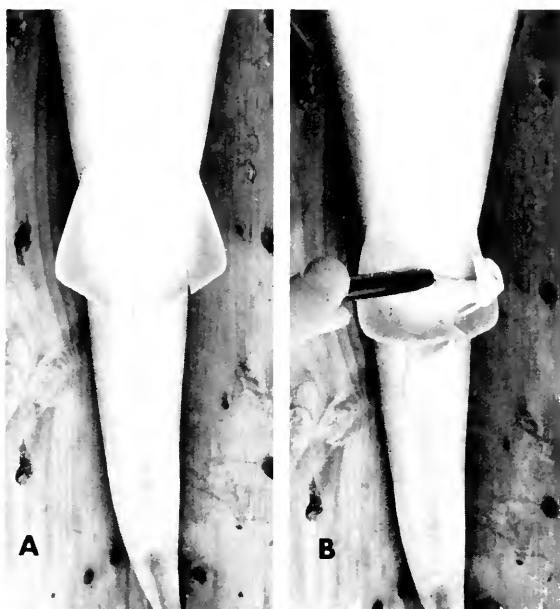


Figure 3. Claspers of the spiny dogfish in (A) resting position and (B) right clasper flexed medially when electrically stimulated, simulating the position after insertion into the female; ventral aspect. (From Gilbert and Heath, 1972)

The distal end of each *ductus deferens* is usually expanded into a sperm storage reservoir, or seminal vesicle, one on each side of the body. In some of the larger sharks, such as the basking shark, *Cetorhinus maximus*, one seminal vesicle may contain 5 to 6 gallons of seminal fluid. I have taken as much as a pint of seminal fluid from the seminal vesicle of a tiger shark, *Galeocerdo cuvieri*, 12 feet in length. During copulation, seminal fluid passes

from the two seminal vesicles into a common chamber and thence through a urogenital papilla into the clasper groove.

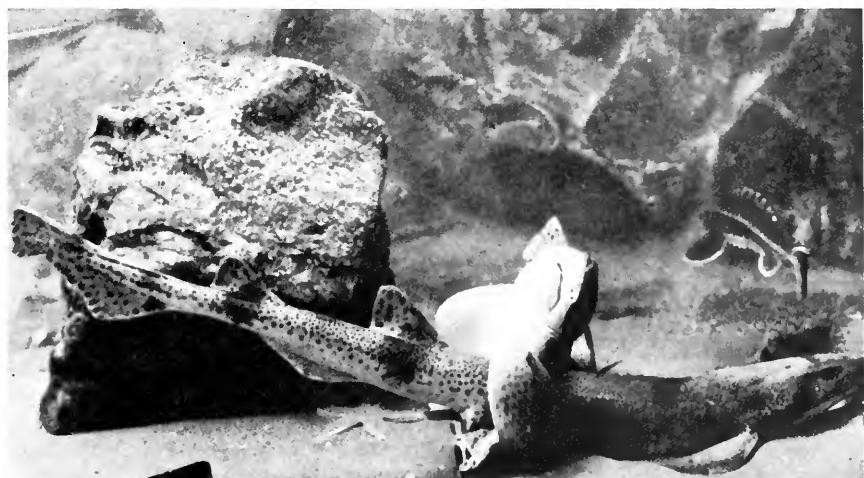
Mating Activities

During courtship, the male of many shark species repeatedly bites the female on her pectoral fins as well as on her back between the two dorsal fins. These areas frequently appear torn or scarred on sharks captured during the mating season. Just prior to clasper insertion, the male usually grasps the trailing edge of the female's pectoral fin in his mouth, and, in some species, such as the catshark, *Apristurus riveri*, the teeth of the male are modified for this purpose. Thus it is possible to sex some species of sharks by their teeth alone.

Relatively few people have actually witnessed the mating activities of any shark. R. P. Dempster and E. S. Herald (1961) described copulation in the hornshark, *Heterodontus francisci*, Eugenie Clark (1963) reported on courtship behavior in the lemon shark, *Negaprion brevirostris*, and R. H. Johnson and D. R. Nelson (1978) described copulation in two common species of tropical Indo-Pacific carcharhinids, the blackfin reef shark, *Carcharhinus melanopterus*, and the reef whitetip, *Triaenodon obesus*. In the classic photograph (Figure 4), taken by F. Schensky in 1914, the male catshark, *Scyliorhinus canicula*, is observed to coil about the female at the time of copulation. In this position, it would be possible to introduce but one clasper at a time. This is the probable mating position in the smaller species of sharks.

Hormone-induced mating behavior. In many vertebrates, a hormone produced by the pituitary gland regulates mating behavior as well as the production of sperm and eggs. It is possible to inject pituitary extract into certain teleosts and cause them to shed their sperm and eggs into the water, where the eggs are normally fertilized. We have frequently

Figure 4. A catshark known as the European spotted dogfish, *Scyliorhinus canicula*, copulating. The male has curled itself about the female and inserted one clasper. This is the probable copulatory position in smaller species of sharks. (Photo by F. Schensky at the Helgoland Aquarium)



tried this method to induce mating behavior in various species of sharks, but these experiments have, for the most part, been unsuccessful.

In 1960, I collected pituitary glands from some large sting rays frequenting the shallow banks of the Bahamas. I carefully removed these pituitaries from the underside of the brain and dried and powdered them. More than 200 milligrams of pituitary powder, suspended in seawater, was then injected into the body cavities of two adult nurse sharks — male and female — at the Miami Seaquarium. After injection, the sharks were tagged and placed in the large oceanarium for subsequent observation. Six other adult male and female nurse sharks in the same tank were used as controls for our experiment. One day later the male and female nurse sharks that had been injected with pituitary extract showed a remarkable interest in each other and swam side by side for the next three days. None of the other sharks showed this behavior pattern, nor had it ever been observed in any of them. While mating was not noted, this behavior was interpreted as part of a mating pattern, for the male would frequently nudge the female and bite the trailing edge of her pectoral fin.

Female Reproductive Structures

Ovary and eggs. The female reproductive tract in all sharks receives semen from the male and consists of a pair of oviducts that join at their forward end to open into the body cavity by a common funnel, or ostium, below the liver (Figure 5). Eggs are produced in the ovaries, or in only the right ovary of many species. When fully formed, the eggs rupture from their ovarian follicles into the body cavity in the vicinity of the ostium. Small, hair-like cells, known as cilia, located on the peritoneal covering of the liver and body cavity in the vicinity of the ovary, create a current of coelomic fluid that moves the eggs forward into the ostium.

Once in the ostium, eggs are forwarded down either oviduct by both peristaltic and ciliary action. Shortly after entering the ostium, the eggs are fertilized by sperm stored in a swollen portion of the upper oviduct known as the nidamental gland. This gland secretes a protective covering about the fertilized egg. In oviparous (egg-laying) sharks this covering is very heavy and is usually dark brown or reddish brown in color. A few deep-water species produce eggs with transparent cases. J. P. Wourms (1977) has found that the egg cases of oviparous sharks are composed of a "unique collagenous protein," organized as a cholesteric liquid crystal.

Oviparous types. The egg cases of oviparous sharks vary greatly in shape and size. The egg case of the Port Jackson shark, *Heterodontus portusjacksoni*, is a cone-shaped structure about 6 inches long with two spiral, screw-like flanges about the outside (Figure 6). It contains a single embryo. R. H. McLaughlin and A. K. O'Gower (1971) believe

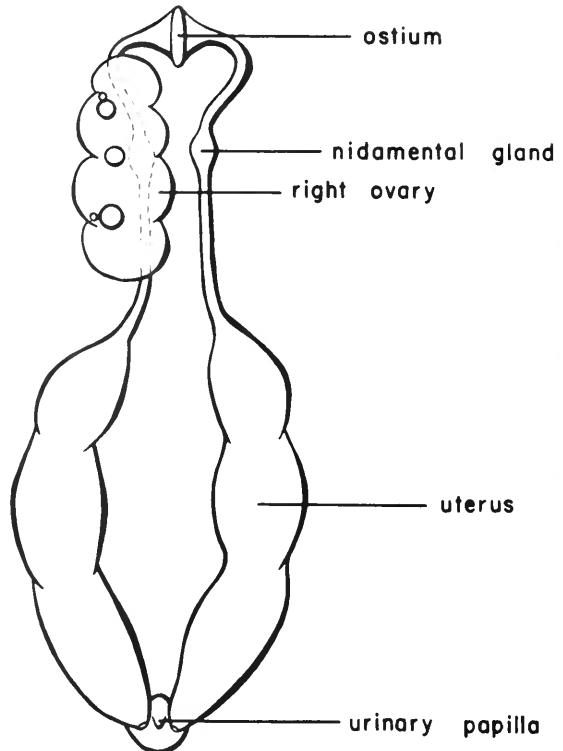
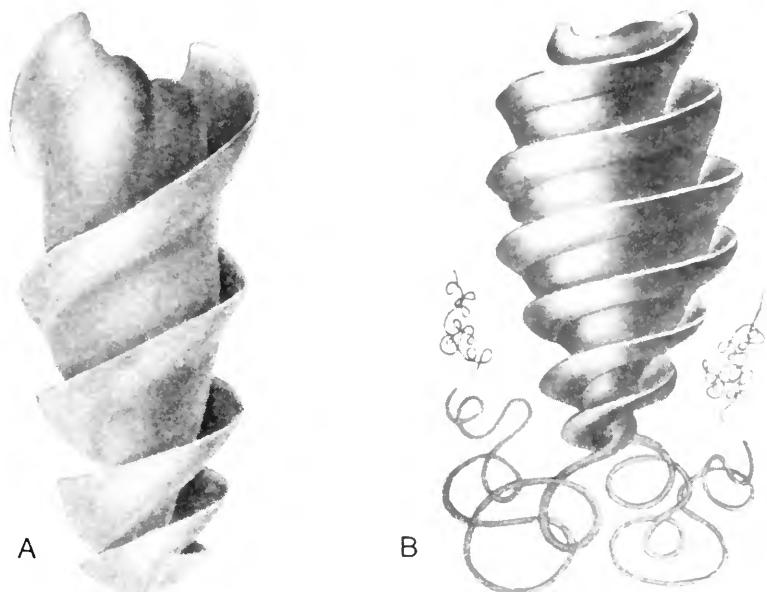


Figure 5. Diagram of female reproductive tract in the spiny dogfish, ventral aspect. The left ovary has been removed. Both ovaries are functional in this species, but in many species of sharks the left ovary is rudimentary and only the one on the right side is functional.

that the female, after extruding an egg, carries the soft egg case in her mouth and places it in a rocky crevice near shore. Because of its screw-like shape, it becomes anchored once it has hardened and thus resists buffeting waves and ocean currents.

Recently (through the courtesy of Lewis H. Bullock at the Florida Department of Natural Resources Marine Laboratory), I obtained the egg cases and developing young of the chain dogfish, *Scyliorhinus retifer*, that were taken in a box dredge at a depth of 750 feet in the Gulf of Mexico. Eggs of this shark are rectangular: 2½ inches long, 1 inch wide, and ¾ of an inch thick. From each corner of the thin, horny egg case, a prominent tendril extends 2 to 3 inches. The case of this deep-water shark is transparent, and one can easily see the large yolk and developing embryo within (Figure 7).

On July 2, 1953, Captain Odell Freeze of the shrimp trawler *Doris*, fishing in the western Gulf of Mexico, obtained a real prize — the egg case of a whale shark, *Rhincodon typus*, containing a live embryo 14½ inches long (Figure 8). The case measured 12 inches long, 5½ inches wide, and 3½ inches thick.



*Figure 6. Egg cases of two hornshark species (A) *Heterodontus francisci* and (B) *Heterodontus galeatus*. (From Daniel: 1934. The elasmobranch fishes, p. 304) The egg case of the Australian hornshark or Port Jackson shark, *Heterodontus portusjacksoni*, described by McLaughlin and O'Gower (1971), is similar to that of *Heterodontus francisci* found in California waters.*



*Figure 7. Translucent egg case and newly hatched young of the chain dogfish, *Scyliorhinus retifer*. (Photo by Robert Pelham)*

Viviparous aplacental types. In contrast to oviparous species, the majority of sharks are viviparous and retain the fertilized eggs in the lower portion of the oviduct known as the uterus. The egg envelopes, secreted by the nidamental gland, are much thinner than the egg cases of oviparous species. In some sharks, such as the spiny dogfish, several fertilized eggs are contained in a single,

thin, amber-colored, horny envelope, known as a "candle" (Figure 9).

In pregnant females, the uterus becomes heavily vascularized to supply the developing pups with oxygen. In some sharks, oxygen is all the pups receive from the mother during development. These shark pups must rely on their enormous yolks for their entire nutriment during their life in utero.

Again, the spiny dogfish is a good example. I have studied the relationship of mother to developing young in this species at the Mt. Desert Island Biological Laboratory in Maine. There, spiny dogfish are found in large numbers during the summer months in the cold waters of Frenchman Bay. The sexes are usually segregated during the summer months; when one fishes in the upper part of the bay one catches pregnant females, while the males are to be found principally in the lower bay, three miles away.

By means of radioisotopes injected into the bloodstream of the pregnant female, G. Bevelander and I were able to follow phosphates and sulphates (substances necessary for the development of the young) from the bloodstream of the mother out into the uterine fluid surrounding the developing pup. Within 12 hours, the radioactive materials passed through the blood vessels of the mother into the cavity of the uterus and literally bathed the young pups in "hot" phosphate or sulphate. After sampling the uterine fluid and determining the amount of radioactive material it contained, we carefully removed the pups one at a time, passed



Figure 8. Young whale shark and egg case from which it was removed. (From J. L. Baugham, 1955)

them through several rinses of distilled water, and then assayed various organs in their body with a Geiger counter. To our surprise, we found that the pups, although they had been bathed for many hours by radioactive phosphate and sulphate, had not picked up these materials and incorporated them into their own tissues. This has led us to conclude that the large yolk sac suspended from the belly and connected to the gut of the spiny dogfish pup contains sufficient nourishment to last it during its prolonged (up to 22 months) gestation period, the longest known for any vertebrate.

Toward the close of the spiny dogfish's gestation period, the yolk sac is gradually resorbed (Figure 10), and at birth the young pup, 8 to 9 inches in length, emerges with a tiny scar on its belly to mark the former position of the yolk sac. After a few weeks, the scar disappears, and no trace remains of the food reserve that nourished the developing pup for a period of nearly two years within the body of its mother.

One of the most unusual patterns of reproduction to be found in sharks is that of the sand tiger, *Odontaspis taurus* — a common shark found off the eastern coastline of the United States

from Cape Cod to Delaware Bay. This species has been successfully maintained for years in large tanks at the New York Aquarium and also at Marineland in St. Augustine, Florida. The sand tiger matures at about 8 feet. Little was known of its reproductive eccentricities until Springer caught one off Chandeleur Island, Louisiana. While conducting an autopsy on a pregnant female, Springer reached into the oviduct, and, to his complete surprise, was bitten by the single sharklet within. An examination of the other oviduct disclosed that it too contained a single pup about 9 inches long and light pink in color. Both pups possessed thread-like, blood-red external gills, which extended outward from each gill slit. The external yolk sac had been completely resorbed. Springer's curiosity was aroused. Over a period of years, he pieced together the following story.

The sand tiger has one enormous ovary which serves both oviducts. The eggs are relatively small, about the size of large peas, and there may be as many as 25,000 in a single ovary. Fifteen or 20 eggs are shed at a time, passing down the oviduct. A thin egg case is secreted about each group of eggs (Figure 11). Presumably the eggs are fertilized in the

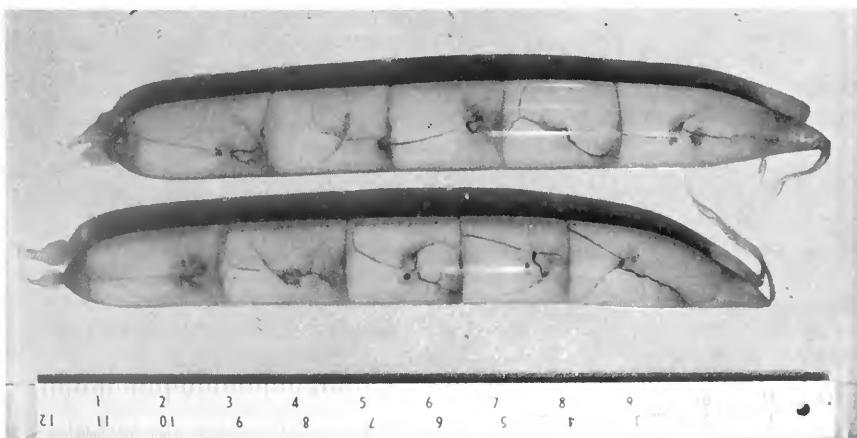


Figure 9. Candle young, two months old, of the spiny dogfish. One candle, enclosing 2 to 6 developing embryos, is found in each uterus of a gravid female. As the embryo grows, the thin candle wall ruptures and the young spend the balance of the 20- to 22-month gestation period within the maternal uteri. (Photo by the author)

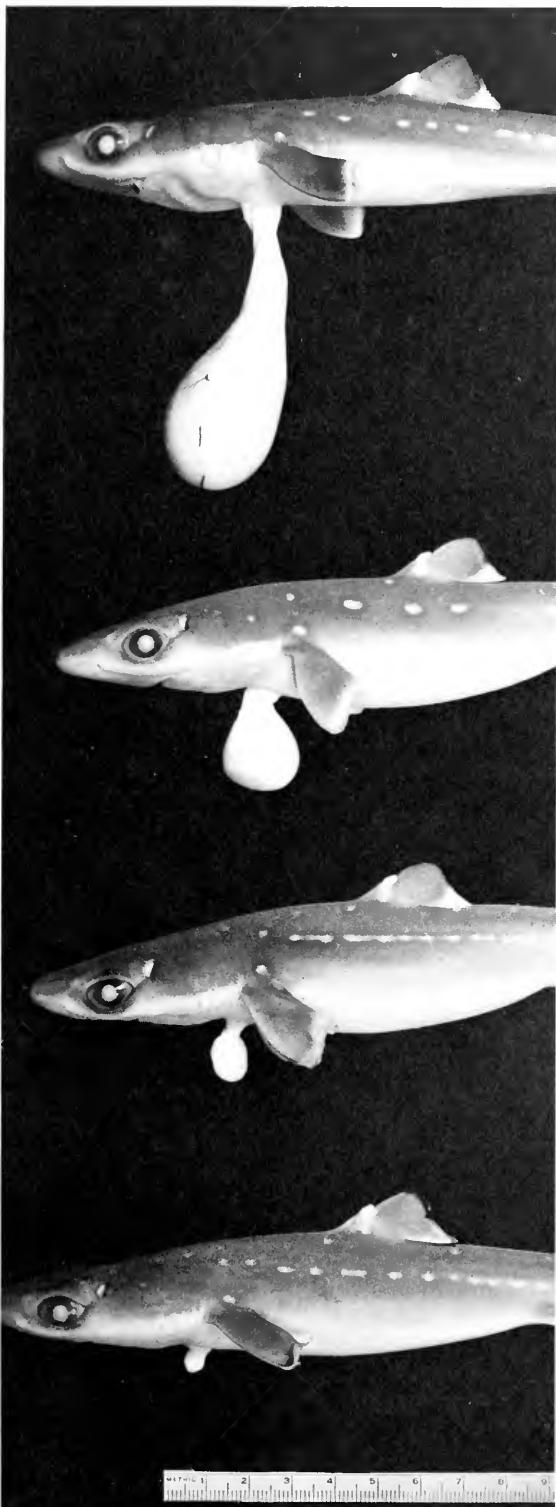


Figure 10. Stages in the resorption of the yolk sac, during the final weeks of the 20- to 22-month gestation period in the spiny dogfish. (Photo by the author)



Figure 11. Egg clusters from the uterus of the sand tiger shark, *Odontaspis taurus*. Each cluster contains 15 to 20 pea-sized eggs and a continuous supply serves to nourish the single pup in each uterus during the greater part of its gestation period. (Photo by Robert Pelham)

upper reaches of the oviduct before they become enclosed in a common case.

As development proceeds, apparently one embryo grows more rapidly than the rest. Its carnivorous appetite spells disaster for its siblings enclosed in the envelope. After that feast, the pup's growth might be seriously impaired were it not for the fact that the ovary sheds forth additional egg cases. These in turn find their way into the oviduct and thence into the mouth of the young predator.

This process of producing eggs in groups of 15 to 20, only to have them consumed by the single shark pup in each oviduct, continues for months until the ovary is completely exhausted of its crop. By this time, possibly after a full year, the growing pup in each uterus has attained a length of 40 inches. This indeed is a respectable length for a shark pup whose mother may measure no more than 100 inches. All this time, the developing pup is oriented in the uterus with its head forward. At birth, however, it somehow turns around in its confined quarters and emerges from its mother head first. Intrauterine cannibalism is also known to occur in mackerel sharks (family Lamnidae) and thresher sharks (family Alopiidae).

Viviparous placental types. In two families of sharks, the requiem (Carcharhinidae) and hammerheads (Sphyrnidae), the developing embryos, after exhausting their yolk supply, depend for the balance of their life in utero on nourishment and oxygen from the maternal bloodstream via a yolk sac placenta. We have studied the placental structure in the silky shark, *Carcharhinus falciformis*, and the Pacific blackfin reef shark, *Carcharhinus melanopterus*. In the silky shark, the vascularized yolk sac wall is but loosely attached to the uterine wall and may be readily peeled away from it (Figure 12). In the blackfin reef shark, however, a portion of the yolk sac wall

becomes so intimately interdigitated with the uterine wall that it is impossible to separate the fetal portion of the placenta from the maternal portion (Figure 13).

The hammerhead shark placentae we have examined — *Sphyrna tiburo*, *S. lewini*, *S. mokarran* — all have similar intimate connections between the fetal and maternal portions. Numerous finger-like processes, known as appendiculae and believed to be respiratory in function, extend outward from the umbilical stalk of *Sphyrna tiburo* and *Sphyrna lewini* but are absent in the great hammerhead, *Sphyrna mokarran* (Figure 14).

This advanced form of nourishing the developing young is analogous to that found in most mammals, for the mother's bloodstream provides nourishment to, and waste removal from, the fetal young. The precise physiological relationship of mother to developing young in placental and aplacental sharks offers a fertile field of investigation. Scant attention has been given this subject since the classic work of S. Ranzi (1932, 1934).

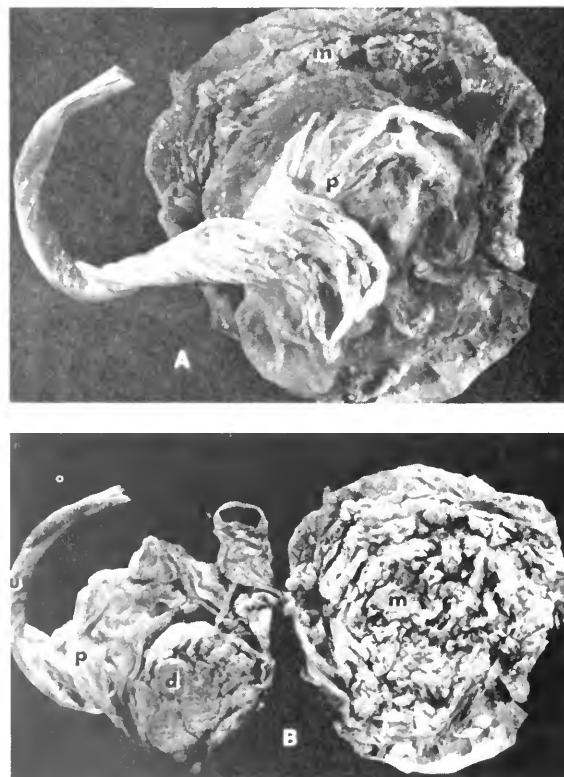


Figure 12. Placenta of the silky shark, *Carcharhinus falciformis*, (A) intact, and (B) with maternal and fetal parts separated; p — proximal region of the yolk sac; d — distal region of yolk sac; m — maternal component of placenta; u — umbilical stalk. (From Gilbert and Schernitzauer, 1966)

Conclusion

In his excellent 1977 paper, Wourms lists eight factors that appear to be important in the evolution of viviparity and retention of oviparity, one of which is the phylogenetic position of the species. "Oviparity is the least specialized and primitive pattern" in sharks and "from it viviparity has independently evolved in several different groups." Of the 16 families of sharks discussed by Wourms, 12 are viviparous or presumed to be, two are oviparous, and in two families both types of reproduction occur. Placental viviparity is confined to two families. Wourms notes that oviparous species are generally benthic, littoral, and not of large size. Viviparous species have more diverse habitats, have larger embryos, grow to larger adult size, and are active predators.

The advantages of viviparity are that the developing young receive protection within the body of the mother and are assured of a constant and stable environment. This form of reproduction culminates in placental viviparity, in which the developing embryo, via its yolk sac, establishes intimate contact with the uterine wall and relies on the maternal bloodstream for nourishment, oxygen, and the removal of wastes.

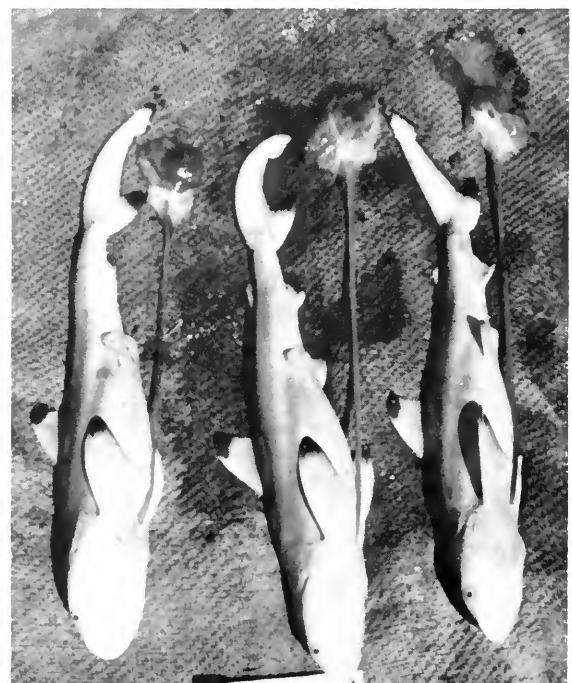


Figure 13. Pups, each with attached umbilical cord and placenta, of the blackfin reef shark, *Carcharhinus melanopterus*. In this species, the fetal and maternal components of the placenta are intimately interdigitated and cannot be manually separated. (Photo by the author at Tikehau, French Polynesia)



*Figure 14. Developing young of the scalloped hammerhead, *Sphyrna lewini* (left) and the great hammerhead, *Sphyrna mokarran* (right). Note the appendiculae, believed to be respiratory in function, associated with the umbilical cord of *S. lewini*. (Photo by Robert Pelham)*

The practice of internal fertilization, coupled with the protection afforded the developing embryo inside a resistant egg case or within the body of the mother, assures a high survival rate during development. Once the young shark emerges from the egg case or the uterus, it must rely on its own sensory and motor systems to locate food and avoid predators. The fact that so many species of sharks have survived for many millions of years is testimony to their reproductive success and to the efficiency of their anatomical equipment.

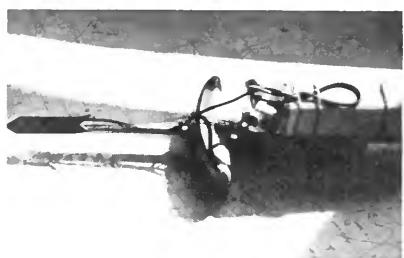
Perry W. Gilbert is Director Emeritus of the Mote Marine Laboratory, Sarasota, Florida, and Professor Emeritus of Neurobiology and Behavior at Cornell University, Ithaca, New York.

Selected Readings

- Baugham, J. L. 1955. The oviparity of the whale shark, *Rhincodon typus*, with records of this and other fishes in Texas waters. *Copeia* 1955 (1), 54-55.
- Breder, C. M., and D. E. Rosen. 1966. *Modes of reproduction in fishes*. Garden City, N.Y.: The Natural History Press.
- Budker, P. 1958. La viviparité chez les selaciens. In *Traité de Zoologie*, P. P. Grassé, ed., Vol. 13, Part 2, 1,755-90. Paris: Masson.
- Clark, E. 1963. The maintenance of sharks in captivity with a report on their instrumental conditioning. In *Sharks and Survival*, P. W. Gilbert, ed., 145-46. Boston: D. C. Heath & Co.
- Dempster, R. P., and E. S. Herald. 1961. Notes on the hornshark, *Heterodontus francisci*, with observations on mating activities. *Occ. Papers Cal. Acad. Sci.* no. 33, 1-7.
- D'Aubry, J. 1963. Elasmobranch reproduction. South African Association for Marine Research, Bull. No. 4, 25-30.
- Gilbert, P. W., and D. A. Schlernitzauer. 1966. The placenta and gravid uterus of *Carcharhinus falciformis*. *Copeia*, 1966 (3), 451-57.
- Gilbert, P. W., and G. W. Heath. 1972. The clasper-siphon sac mechanism in *Squalus acanthias* and *Mustelus canis*. *Comp. Biochem. Physiol.* 42A: 97-119.
- Johnson, R. H., and D. R. Nelson. 1978. Copulation and possible olfaction-mediated pair formation into two species of carcharhinid sharks. *Copeia*, 1978 (3), 539-42.
- McLaughlin, R. H., and A. K. O'Gower. 1971. Life history and underwater studies of heterodont sharks. *Ecol. Monographs* 41: 271-89.
- Ranzi, S. 1932. Le basi fisio-morfologiche dello sviluppo embrionale dei Selaci — Parte I. *Pubb. Staz. Zool. Napoli*. 13: 209-90.
- 1934. Le basi fisio-morfologiche dello sviluppo embrionale dei Selaci — Parte II e III. *Pubb. Staz. Zool. Napoli* 13: 331-437.
- Schlernitzauer, D. A., and P. W. Gilbert. 1966. Placentation and associated aspects of gestation in the bonnethead shark, *Sphyrna tiburo*. *J. Morph.*, 120: 219-31.
- Springer, S. 1960. Natural history of the sandbar shark, *Eulamia milberti*. *U.S. Fish Wildl. Serv. Fish. Bull.* 61: 1-38.
- Wourms, J. P. 1977. Reproduction and development in Chondrichthyan fishes. *Amer. Zool.* 17: 379-410.



1 sharing fishing information



2 harpoon dart with transmitter



3 chum



4 blue shark taking chum



5 locating more blue sharks



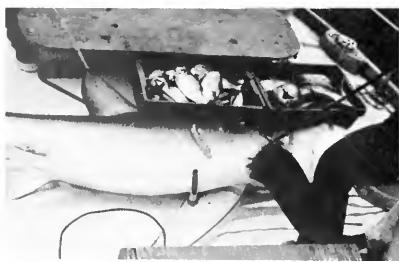
6 ready to harpoon



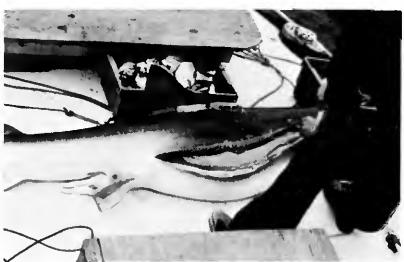
9 ready to come aboard



10 starting to haul aboard



13 shark with two transmitters



14 opening belly to remove stomach

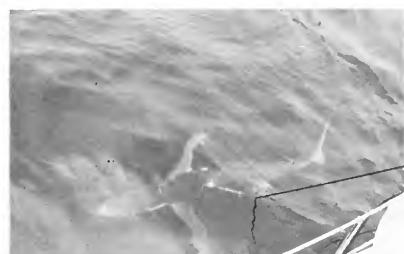
Telemetry and Blue Sharks

Photos by E. Kevin King

These photographs were taken during research conducted by Dr. Francis G. Carey of the Woods Hole Oceanographic Institution and by Fisheries biologist Nancy Kohler of the National Marine Fisheries Service, Narragansett, Rhode Island, aboard the 50-foot motor sailer Bird of Passage in July 1980, in waters south of Martha's Vineyard, Mass. Chum was used to attract blue sharks, *Prionace glauca*, and after one particular shark was chosen it was fed whole mackerel and tagged with two transmitters, one for depth and the other for temperature. The shark's movements were recorded every 5 minutes, and after a specified period the shark was located, harpooned, and landed (photo sequence). The stomach was removed and measured for weight, volume, content, and rate of digestion of the mackerel.



7 harpooning



8 harpoon placed



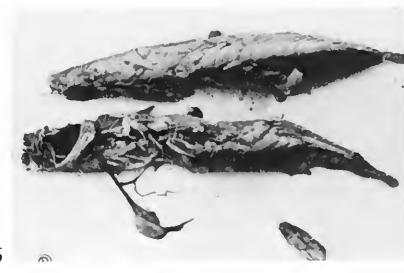
11 checking deck space



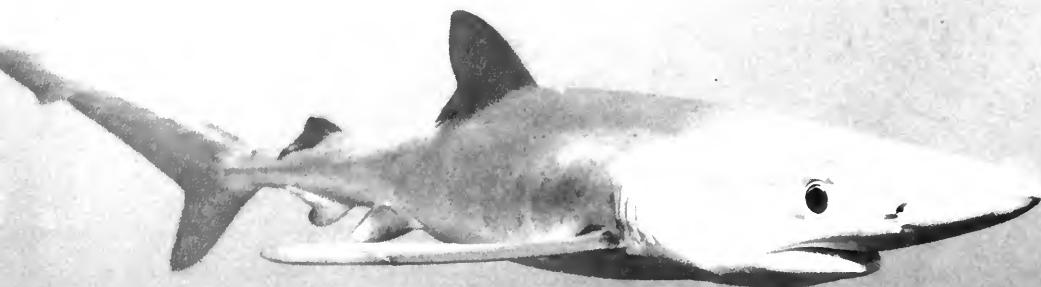
12 blue shark aboard



15 six 10-hour mackerel and a normal one



16 two 26-hour mackerel



Electroreception in Blue Sharks

Photo by Marty Snyderman

by Paul R. Ryan

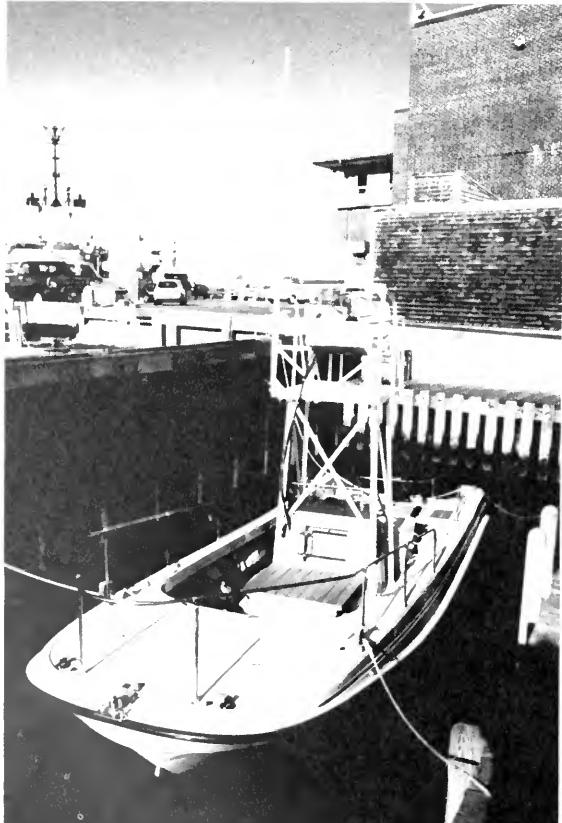


Figure 1. The Boston Whaler from which research was conducted on the blue sharks, *Prionace glauca*. (Photo by Gail W. Heyer)

Do sharks seeking food in the open sea home in on the weak electric fields of their prey? Does the sharks' electric detection system—one of the most remarkable in all nature—also aid the animals in the process of daily movement as well as long-range migration, allowing them to orient in the open sea electromagnetically?

To answer the first of these questions, Dr. Adrianus J. Kalmijn, a specialist in sensory biophysics at the Woods Hole Oceanographic Institution, arranged a series of expeditions to the shark-inhabited waters off Cape Cod. During last summer, Gail W. Heyer, Melanie C. Fields, and R. Douglas Fields joined the research effort.

Working at night from a 21-foot Boston Whaler (Figure 1) in 40 meters of water, approximately 25 kilometers south of Martha's Vineyard, they endeavored to test the oceanic blue shark, *Prionace glauca*, on its behavioral responses to electrically simulated prey.

In previous work, under contract with the U.S. Office of Naval Research, Kalmijn had demonstrated that the bottom-dwelling, shallow-water shark *Mustelus canis*, the common smooth dogfish, can detect minute electrical voltage gradients as small as five-thousandths of a microvolt (= 5 nanovolts) per centimeter. This degree of electrical sensitivity is by far the highest known in the animal kingdom. It enables dogfish sharks—and the kindred skates and rays—to locate prey, such as small flounder buried beneath

the sand, by the weak DC and low-frequency bioelectric fields that all aquatic animals produce.

The Blue-Shark Studies

The team first made a few trips to locate a desirable research site for the blue shark studies and to adapt the shallow-water gear to the open-ocean work. During spells of relatively calm seas, four long nights were spent drifting on the water, one of which yielded most of the observed feeding responses. For safety reasons, the crew maintained radio contact with a nearby fishing boat.

A current source and two pairs of salt-bridge electrodes, each located 30 centimeters from a central odor source (Figure 2), produced the electric fields to simulate the prey. The electrodes and odor source were suspended 5 meters beneath a glass viewing well in the bottom of the fiberglass research vessel,* which was designed to provide a working platform free of galvanic fields. A single underwater light, positioned near the water surface, dimly illuminated the observation area — just enough to see the sharks, without noticeably disturbing them.

The blue sharks observed ranged in size from about 2 to 3 meters. Slender, of a shiny "metallic" blue color, they commonly roam and feed in the top layer of the water column and are noted for their keen sense of sight and smell.

A direct current of 8 microamperes was applied to one or the other of the electrode pairs to represent the prey. With the electrodes 5 centimeters apart, the current gave rise to a dipole field decreasing to 5 nanovolts per centimeter within a radius of 24 to 30 centimeters from its source. The electrode pairs were embedded in two yellow sponges to provide the sharks with distinct targets.

To attract the sharks to the observation area, small amounts of menhaden chum were pumped through the odor port between the two electrode pairs. According to a random sequence, one dipole was activated while the other served as the control for equal trial periods.

During the most active night, five sharks attacked the test apparatus a total of 40 times, with 2 bites at the odor source, 7 on the unactivated dipole, and 31 on the activated dipole. On the other less calm test nights, nine bites were recorded at the electrically simulated prey and only one bite at the control electrodes. As far as statistical methods may be applied to the data, the researchers conclude that the blue sharks show a highly significant preference for the current-carrying electrodes. Thus, despite concurrent olfactory and visual cues, the oceanic blue sharks will execute typical feeding

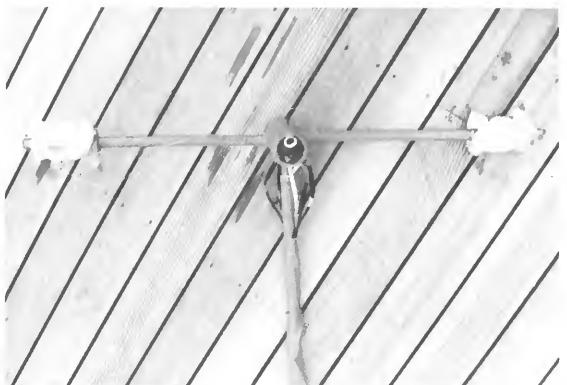


Figure 2. Dipole apparatus. Electrode pairs are embedded in two yellow sponges and separated by odor port at center. (Photo by Gail W. Heyer)

attacks in response to electric fields simulating prey.

The results of Kalmijn's research indicate that attacks on humans and underwater equipment may also be elicited and guided by electric fields resembling those of prey. The human body, especially when the skin is damaged, creates DC bioelectric fields that sharks in the ocean can detect from distances up to at least one meter. The galvanic fields of metallic objects are usually even stronger and may either attract or, for that matter, confuse the animals. This could explain much of the aberrant behavior of sharks in the presence of man and underwater gear.

A Compass Mechanism?

Sharks, skates, and rays detect the low-level electric fields with the ampullae of Lorenzini — delicate sensory structures (Figure 3) in the protruding snouts of these elasmobranch fishes.

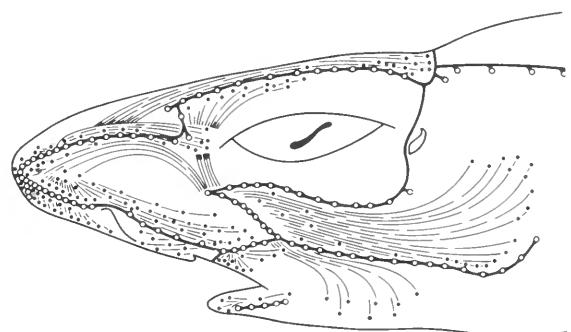


Figure 3. Ampullae of Lorenzini and mechanical lateral-line system in head region of the shark *Scyliorhinus canicula*. Solid dots: skin pores of electroreceptors. Small circles: openings of lateral-line canals. (After Dijkgraaf and Kalmijn, 1963)

*The boat was built through a grant from the Eppley Foundation for Research.

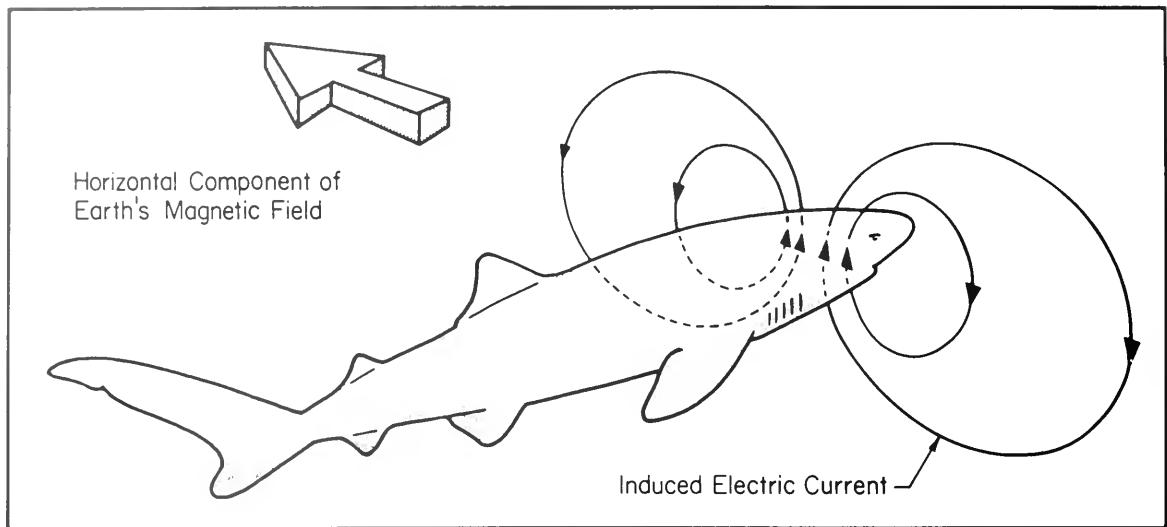


Figure 4. A shark swimming through the earth's magnetic field induces electric fields giving the animal's compass heading. (From Kalmijn, 1974)

Wind-driven and tidal ocean currents flowing through the earth's magnetic field induce electric fields that are perpendicular to and, in the Northern Hemisphere, directed to the left with respect to the flow of water. When measured with towed electrodes, the voltage gradients range from 0.05 to 0.5 microvolts per centimeter. In these fields, marine elasmobranchs may orient electrically, either to compensate for passive drift or to follow the ocean currents during migration. In fresh water, the prevailing electric fields are much stronger and of electrochemical rather than electromagnetic origin, offering more local, territorial cues. Over the years, Kalmijn has demonstrated the animals' ability to orient with respect to these inanimate, environmental fields. Thus, in well-controlled laboratory experiments, the stingray *Urolophus halleri* learned to procure food from a plastic corral to the right with respect to a uniform electric field and to avoid a similar enclosure to the left with respect to the field. The stingrays were able to locate the "correct" corral down to the same threshold gradient as was found in the studies on the sharks' feeding responses.

When actively swimming through the earth's magnetic field, sharks, skates, and rays induce local electric fields of which the voltage gradients depend on the fishes' compass headings (Figure 4). As these fields are strong enough to be detected at swimming speeds of only a few centimeters per second, the elasmobranchs could, in addition, be endowed with an electromagnetic compass sense. They not only receive the electrical information, but also are readily trained to orient with respect to the earth's magnetic field. Natural scientists have often wondered whether animals, in particular migrating

birds and fish, might not direct themselves to the earth's magnetic field. Sharks certainly could, and we may even know their detection mechanism. By the same token, biological organisms could also use the principle of the magnetic compass needle, as has been recently demonstrated for bacteria (see *Oceanus*, Vol. 23, No. 3, p. 55).

Paul R. Ryan is Managing Editor of Oceanus magazine, published by the Woods Hole Oceanographic Institution.

Acknowledgment

The author would like to acknowledge the help and advice given in the preparation of this article by Dr. Adrianus J. Kalmijn, presently at the Scripps Institution of Oceanography, University of California, San Diego.

Further Reading

- Clark, E. 1981. Sharks: magnificent and misunderstood. *National Geographic magazine*, 160: 138-87.
- Heyer, G. W., M. C. Fields, R. D. Fields, and A. J. Kalmijn. 1981. Field experiments on electrically evoked feeding responses in the pelagic blue shark, *Prionace glauca*. Short communication in *Biol. Bull.*, October issue.
- Kalmijn, A. J. 1974. The detection of electric fields from inanimate and animate sources other than electric organs. In *Handbook of Sensory Physiology*, vol. III/3, A. Fessard, ed., pp. 147-200. Berlin-Heidelberg-New York: Springer-Verlag.
- . 1977. The electric and magnetic sense of sharks, skates, and rays. *Oceanus*, vol. 20, no. 3.
- . 1978. Electric and magnetic sensory world of sharks, skates, and rays. In *Sensory Biology of Sharks, Skates, and Rays*, E. S. Hodgson and R. F. Mathewson, eds., pp. 507-528. Washington, DC: Government Printing Office.
- . 1981. Biophysics of geomagnetic field detection. *I.E.E.E. Trans. Magnetics*, 17: 1113-24.
- Ryan, P. R. 1980. Geomagnetic guidance systems in bacteria, and sharks, skates and rays. *Oceanus*, vol. 23, no. 3.

Aggression in Sharks:

Is the Gray Reef Shark Different?

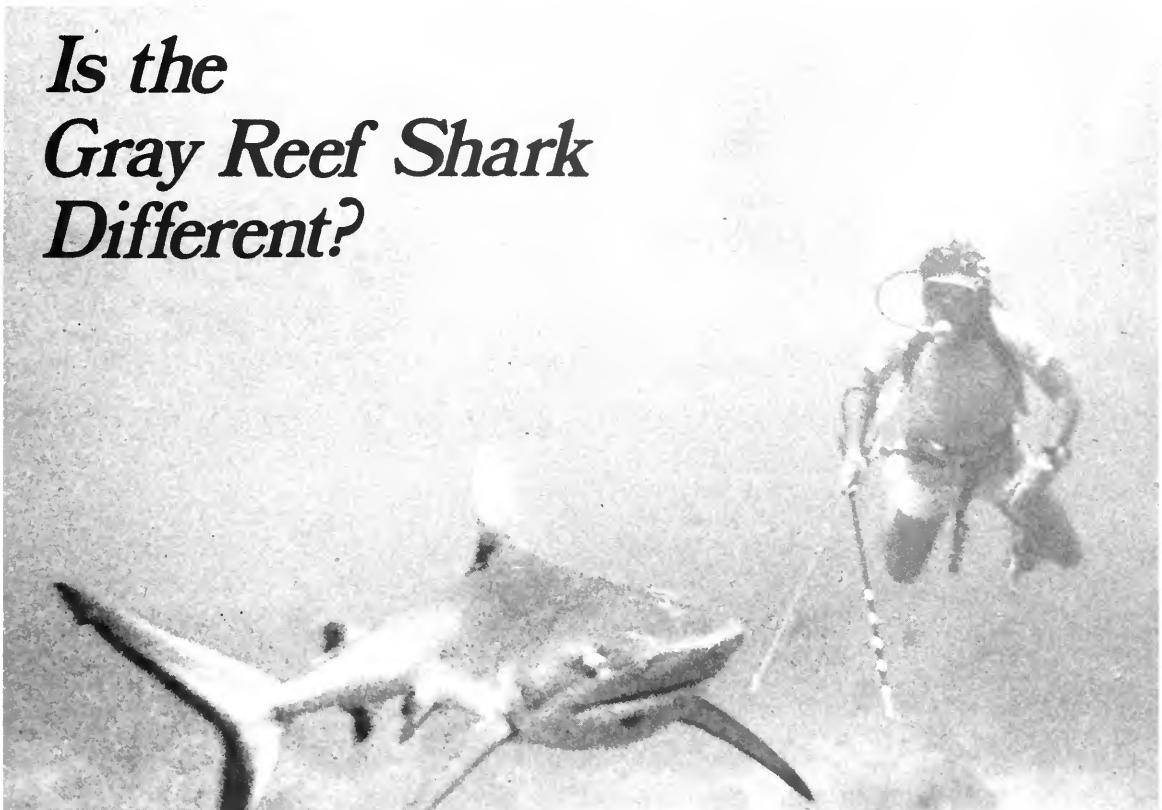


Figure 1. The gray reef shark, *Carcharhinus amblyrhynchos*, an aggressive shark of the tropical Indo-Pacific region. It is known to threaten and attack skin divers. (Photo by J. McKibben)

by Donald R. Nelson

Most shark species do not appear to be very aggressive. This may seem surprising in view of the popular image of sharks as voracious predators. Many sharks are indeed voracious feeders, but predation and aggression are not the same.

In the strict behavioral sense of the word, "aggression" refers to fighting in defense of self or of resources considered valuable. Scientists distinguish between social aggression — fighting against competitors (usually of the same species) for resources such as space, food, or mates — and antipredatory aggression, fighting off predators (usually of other species) to save oneself or one's offspring. Predation, killing to obtain food, is considered separate from aggression by most ethologists.

If one observes most kinds of sharks in nature or in large enclosures, one rarely sees overt aggression between individuals, such as threats, attacks, or chases. Even during active feeding, each shark seems interested only in getting directly to the food, without threatening or attacking competing sharks. Such *scramble* competition can be likened to football players chasing a fumbled ball, and is distinctly different from *contest* competition, where access to a desired item is earned by winning an aggressive interaction, like boxers competing for a trophy. Exceptions to this have been noted, and will be discussed later, but thus far they have been relatively few.

In 1970, University of Miami scientists Arthur Myrberg and Samuel Gruber studied a group of 10

bonnethead sharks, *Sphyrna tiburo*, in a semi-natural pool at the Miami Seaquarium. They made a point of mentioning the "relative lack of belligerency" among members of the group, and that aggression between individuals was "not seen during competition for limited food." In more than 200 hours of observation during a six-month period, no active fighting was seen. However, they did see several cases of "hits" by one shark on another, and a behavior they called the "hunch"—both of which occurred most often when a newcomer was added to the pool. Myrberg and Gruber were also able to show that a subtle, size-dependent dominance hierarchy existed in the group. Since few aggressive behaviors occurred, they established the hierarchy by watching "give-ways," where one shark altered its course to avoid a head-on collision with another.

From observations such as these, we are left with the impression that, *intraspecifically* (within a species), sharks lead relatively peaceful lives in comparison to many other vertebrates. Numerous species of mammals, birds, and reptiles are overtly much more aggressive than sharks; and so are many fishes, such as the little damselfishes of tropical coral reefs. Aggressive behaviors in these other animals, however, are most obvious at times when they are defending territories, mates, or offspring. None of these behaviors has yet been observed in sharks. Is this because they do not exist, or because sharks in the wild are very difficult to observe? For instance, copulation is one behavior that we know exists, yet has never been observed in the great majority of active, dangerous sharks.

Attacks on Humans: Feeding or Fighting?

What about *interspecific* aggression? How do sharks interact with other species, including man? There is very little data, but certain observations indicate that some species show dominance over others. From a vessel at sea, fishery biologist Stewart Springer observed feeding in a mixed aggregation of similarly sized silky sharks, *Carcharhinus falciformis*, and oceanic whitetip sharks, *C. longimanus*. "When competition for a tidbit was between a whitetip and a silky shark at close quarters, the silky shark gave way to the whitetip shark, but, when the competition was between two whitetips or two silky sharks, both appeared to close in on the food without reluctance," Springer wrote. Does the existence of a subtle "dominance" in a species indicate that it might be capable of more aggressive actions—such as attacking other sharks or humans? Perhaps, but more evidence is needed before we can say this for sure.

What can be learned from statistics on shark attacks on humans? The International Shark Attack File (SAF) is a collection of more than 1,600 case histories obtained from eyewitness accounts, newspaper articles, medical records, and other

reports. Working at the Mote Marine Laboratory in Sarasota, Florida, U.S. Navy Captain H. David Baldridge undertook a thorough analysis of SAF data, using 1,165 cases which were judged complete enough for computer coding. An important point that emerged from this analysis is that not all attacks appeared to be motivated by hunger, as was once more or less assumed. Baldridge and J. Williams, in their 1969 paper "Shark attack: feeding or fighting?", pointed out that many victims bore wounds of the "slash" type that did not seem consistent with an attempt to remove flesh. They concluded that as many as 50 to 75 percent of the SAF cases could have been non-hunger motivated, perhaps the "results of aggressive behavior directed at victims in an attitude of fighting rather than feeding."

Is it possible that sharks in general are really more aggressive than previously suspected, and that we simply have not been able to observe them at the appropriate times and places? The answer is probably yes, but there is one notable species, the gray reef shark, for which we do have direct experimental evidence of attacks based on true aggression rather than feeding.

The Gray Reef Shark

In the tropical Indo-Pacific region, around the coral atolls of Polynesia and Micronesia, there is one shark that skin divers have learned to be wary of—the gray reef shark, *Carcharhinus amblyrhynchos* (=menisorrah: Figure 1). Although reaching only about 2 meters in length, it is the boldest, most aggressive shark of the area, appears dominant over other reef species, and has attacked divers on a number of occasions. It also is one of the most social sharks, in terms of grouping behavior. Study of this species has been one of the major efforts of our shark research program at California State University, Long Beach.

Significantly, nearly all attacks by gray reef sharks have been prefaced by a distinct exaggerated-swimming display. This strange body language was first studied in detail in 1971 by Richard H. Johnson and myself while working out of the marine laboratory (presently called the Mid-Pacific Research Lab) at Enewetak, Marshall Islands. A type of agonistic display (threat display), it consists of a tense, laterally exaggerated swimming with the back arched, snout raised, and pectoral fins lowered (Figure 2). Among other things, it was determined that an "aggressive" approach by the diver could trigger the display, especially if the shark was in any way cornered.

The gray reef sharks of Enewetak are particularly bold and have a habit of making close investigatory passes at scuba divers. It can be disconcerting to a diver to see a shark approach out of the distant blue, swim directly at him, and circle

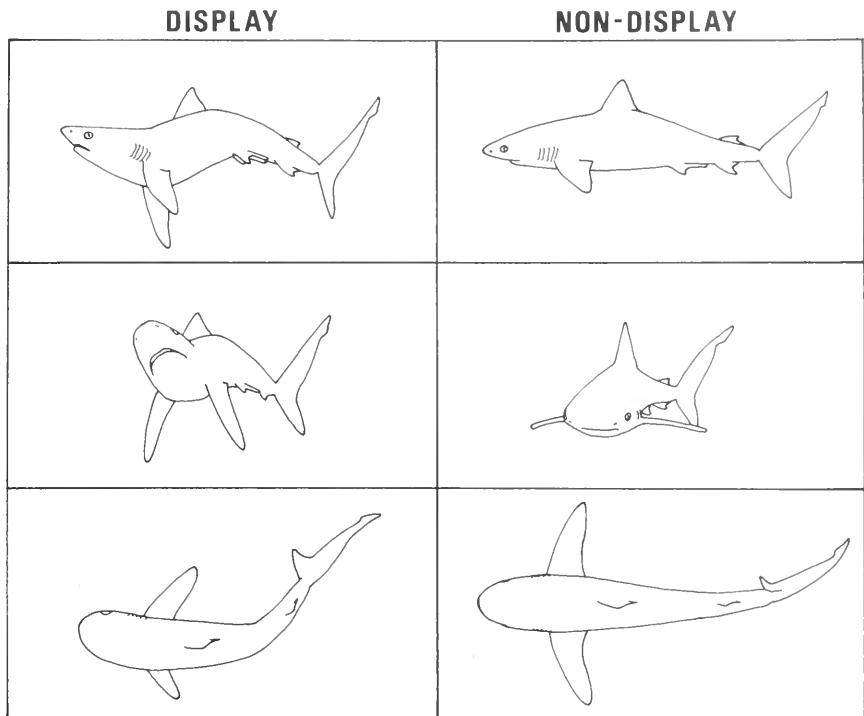


Figure 2. Comparison of threat display postures (left) and ordinary swimming (right) in the gray reef shark. Note the arching of the back, lifting of the snout, and lowering of the pectoral fins. (From R. H. Johnson and D. R. Nelson, 1973; with permission of Copeia)

him excitedly at arm's reach. If many sharks are present, as occurs at some places along the ocean-reef dropoff, the diver may find himself the center of attention for a dozen or more sharks. Aggressive as these sharks may seem, however, full threat displays are usually not seen in this situation. If the diver remains calm and "defensive," the sharks will eventually disperse without incident. We noticed, however, that if one of us swam rapidly toward an approaching shark, especially one just arriving, the shark would almost invariably go into exaggerated-swimming behavior. We made 10 experimental approaches to sharks in this way and obtained some degree of display in each case. If we managed to partially corner the shark, the display became more intense (Figure 3). Since the behavior was clearly related to provocation by the diver, and since we knew of one case where it did precede an attack, we concluded that it probably represented defensive threat.

Attacks on Divers and Submersibles

Although Johnson and I did not fully realize it at the time, we came very close to being attacked during our 1971 experiment. Shortly after our Enewetak study, we learned of several more attacks by gray reef sharks on divers and on a small submarine. All involved the exaggerated-swimming display. As a result of these incidents and further experiments, it is now clear that if a diver approaches a displaying

shark too closely, it will quite likely launch a sudden, high-speed strike. These attacks are so fast that defense is nearly impossible, and the resulting bites or slashes can produce severe wounds requiring emergency treatment, hospitalization, and reconstructive surgery.

The first agonistic attack by a gray reef shark that we know of occurred at Wake Island in 1961, and was well documented by Ron Church in an article in *Skin Diver* magazine. Church and Jim Stewart, the diving officer at Scripps Institution of Oceanography, were free-diving on the ocean reef, checking out a wave-height recording instrument. The shark was swimming along a coral ravine and passed between the two divers, whereupon they both made moves at it — triggering the exaggerated-swimming behavior. After the display, the shark abruptly turned and made a lightning-fast attack on Stewart, delivering two severe bites just above the elbow. Although the article described the shark as a "black tip," a photo Church took seconds before the attack clearly identifies it as a gray reef shark, in agonistic display.

Another attack occurred at Enewetak in 1976 and was witnessed by John Randall, an ichthyologist from the Bishop Museum, Honolulu. Randall and Shot Miller were scuba diving in about 20 meters of water near the deep entrance channel to the lagoon. Miller had a powerhead weapon and was "riding shotgun" above Randall in order to protect

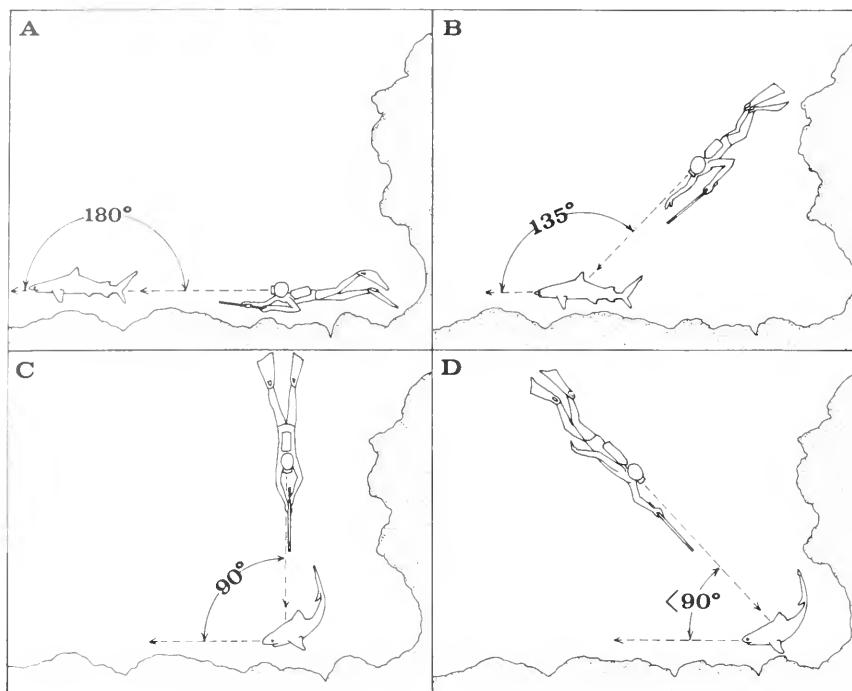


Figure 3. The effect of cornering on the intensity of threat display in the gray reef shark. In situation D (strong cornering), an approaching diver is more likely to trigger an intense display — and be attacked — than in situation A (no cornering). (From R. H. Johnson and D. R. Nelson, 1973; with permission of Copeia)

him from sharks. As described by Randall (quoted in *The Book of Sharks* by Richard Ellis), "A gray reef shark came up behind me and started its threat posturing. Shot whacked his scuba tank with his powerhead shaft to warn me. The shark (which was only about 4.5 feet) then veered to him and threatened him even more strongly, the head moving thru an arc of nearly 180 degrees. — He didn't have time to look at the shells as the shark closed on him too rapidly — he picked the old (wrong) shell and it misfired as he struck the shark's head with it. It came right on and bit him on the head on one side — cut off his face mask and he headed right for the surface. Shot had seven gashes that required 25 stitches to close. It was only the result of a slash with the upper jaw."

Perhaps the worst gray reef shark incident occurred in 1978 at Enewetak on a pinnacle reef near the center of the lagoon. One five-foot shark attacked two scuba divers, laboratory manager Michael deGruy and his partner Phil Light. The actual strike was apparently triggered when deGruy took a flash photo of the threat-displaying shark from about 6 meters away. As described by deGruy, "Immediately the shark broke its awkward posture, turned, and began swimming directly toward deGruy at a high rate of speed. Before deGruy even lowered his camera from his eye, the shark was half-way to him. Not having time to get to his bang stick (powerhead), he reacted by shoving his camera into the face of the oncoming shark." The charging

shark knocked the camera aside, "opened its mouth and closed it around deGruy's upper right arm, elbow, and forearm. Exerting clamping pressure on the arm, the shark began shaking its body and head, tearing muscle, tissue, and skin from deGruy's arm." After releasing his arm, the shark quickly circled back and bit deGruy's swim fin, removing a chunk of rubber. Phil Light moved in with his multi-pronged "shark billy," but the shark attacked him also, raking his left hand with its lower teeth, then grasping the billy in its mouth and shaking it violently before releasing it and swimming away. Both divers were evacuated to the U.S. Navy Hospital in Guam, and later transferred to Honolulu for surgery.

Not only have gray reef sharks attacked divers, but they have also struck small diver submarines. In the late summer of 1971, about six months after the Johnson/Nelson study, marine biologist Walter A. Starck II arrived at Enewetak on his own vessel. He had with him a two-person submersible called the Perry Sharkhunter. Starck had previously seen movie footage that Johnson and I had taken of the displaying gray reef sharks. He soon recognized that the Enewetak grays would respond aggressively to the submarine if pursued, even at relatively slow speed. Not only did the sharks threat-posture at the sub; some eventually attacked it. Rhett McNair, then laboratory manager at Enewetak, was with Starck in the sub one day and described what happened when they followed one

shark in intense display: "The shark moved slowly ahead of us in this attitude for perhaps 30 seconds before exploding into an incredibly fast back loop which brought it crashing straight down onto the half-inch-thick plexiglass hood a few inches over our heads. The deep scratches on the hood clearly showed that both upper and lower teeth bit the plexiglass. . . ." From this attack and others like it, it became evident that gray reef sharks would not hesitate to attack adversaries many times larger than themselves.

Experimentally Induced Attacks

It was clear that the threat and attack behaviors of the gray reef shark were very relevant to an overall understanding of the problem of shark attack on humans. It also was obvious that it was too risky for unprotected divers to attempt to study this behavior, so our California State University group set out to build a bite-proof diver vehicle specifically for experiments on shark aggression. Designed and built by Robert R. Johnson and myself, the one-man, fiberglass Shark Observation Submersible (SOS) was smaller, faster, and more maneuverable than the two-person sub previously used at Enewetak (Figure 4). The streamlined SOS has an acrylic-dome entry port at the forward end which also provides excellent visibility for the diver lying prone within. The scuba air supply, battery pack, and foam flotation are mounted inside. The three electric motors, two forward "pectoral fins," and aft tail fin are all independently controllable by the operator. The craft can be launched from a small boat, using a special aluminum-rail launching ramp.

Initial experiments on gray reef sharks were conducted at Enewetak in 1977 and 1978 by Robert Johnson, James McKibben, Gregory Pittenger, and myself. A total of 10 attacks on the SOS were elicited, several being double strikes, and several causing minor damage to the sub. Typically, exaggerated-swimming display was triggered by an



Figure 4. The author with the Shark Observation Submersible as used at Enewetak, Marshall Islands, in 1978. The streamlined, fiberglass craft is 8 feet long and 2 feet in diameter. It is entered underwater by removing the forward acrylic-dome port. (Photo by J. McKibben)



Figure 5. A gray reef shark performing exaggerated-swimming display in response to the submarine. In this case, the shark is "carouselling" (circling with) the sub, and is making no apparent effort to escape. (Photo by J. McKibben, from 16mm movie footage)

"oriented pursuit" — the sub following the shark's every move (Figure 5), especially if this resulted in some degree of cornering. The shark would then slow down, intensifying its display as the sub neared. The attack itself usually came when the sub had closed to about 2 meters, by which time the shark had often begun to roll somewhat on its side in a very tense, contorted posture. The strikes were incredibly fast. In one attack filmed by *Wild Kingdom* photographer Ralph Nelson, the shark took only .33 of a second to hit the sub, biting the forward motor and breaking the plastic propeller (Figure 6).

Experimental trials were run to test the effects of 1) presence of bait, 2) grouping type, 3) location on reef, and 4) species of shark. Gray reef sharks would attack either with or without bait present, but seemed more attack-prone if they were already at the test site and did not have to be baited in. Lone individuals seemed more prone to display and attack than those in aggregations or schools. Attacks occurred over flat reef bottoms and along steep dropoffs (Figure 7). Significantly, all of the attacks were by gray reef sharks (both sexes). Neither attack nor full display could be elicited from silvertip sharks, *Carcharhinus albimarginatus*; blackfin reef sharks, *C. melanopterus*; or reef whitetips, *Triaenodon obesus*.

a



b



c



d



e



f



Figure 6. Agonistic attack by a gray reef shark on the approaching submarine. Note the extreme rolling and intense posture just prior to attack. Shark bit motor and broke plastic propeller, disabling sub. (Photos by R. Nelson, from 16mm frames, courtesy of Don Meier Productions)

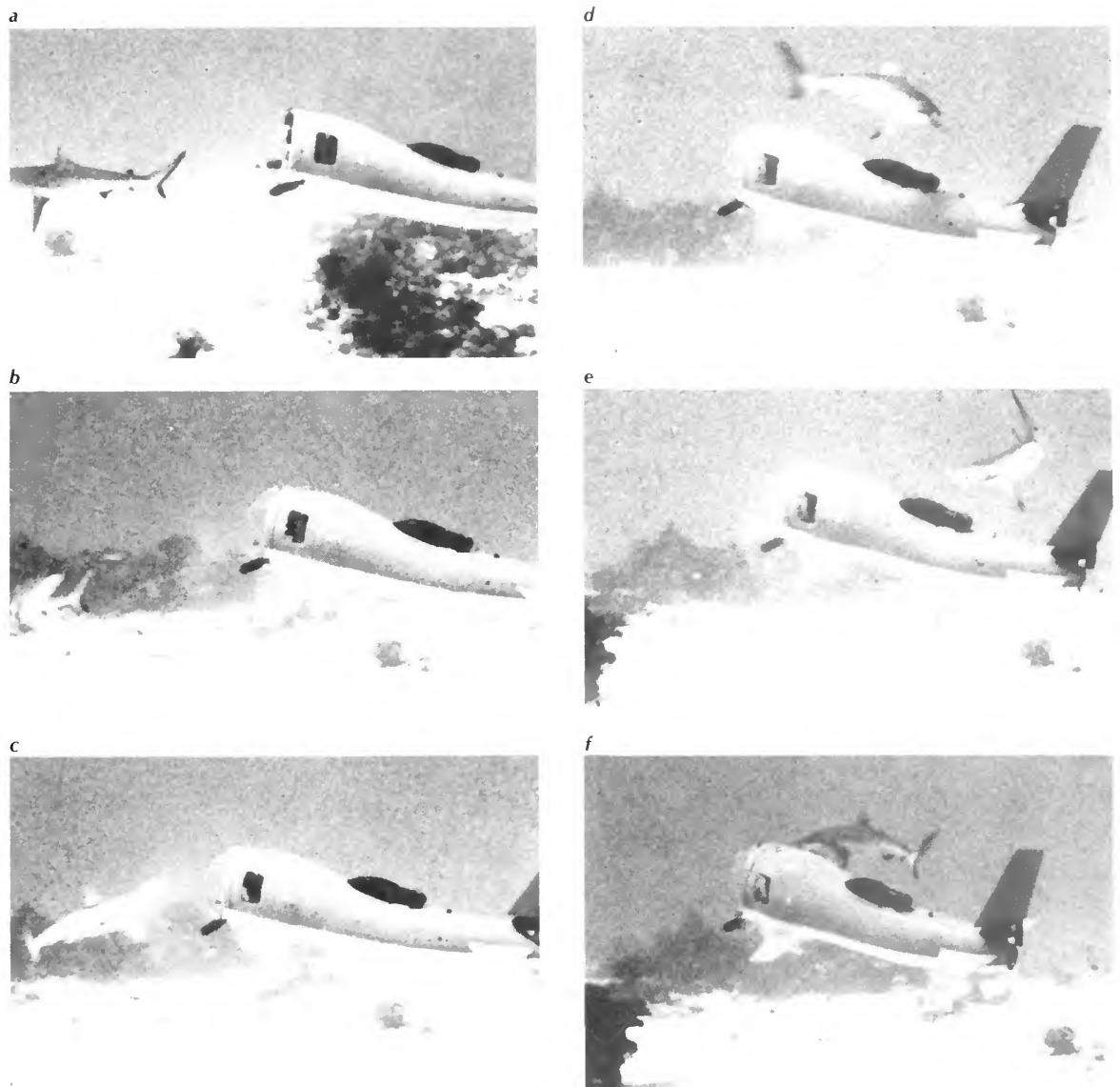


Figure 7. Attack from the rear by a gray reef shark at Enewetak in 1978. The shark avoided a direct frontal attack, instead circling around and striking from behind. (Photos by A. Giddings, from 16mm footage, courtesy of Hessischer Rundfunk, Frankfurt, West Germany)

Attack Motivation

Why do gray reef sharks attack divers and submarines? The sharks are certainly not trying to eat the subs. Furthermore, the exaggerated-swimming behavior is very conspicuous — exactly the opposite of what would be expected prior to a feeding-motivated attack. No predator forewarns its prey of its intent to attack. The real question is whether the shark regards the sub or diver as a competitor for food or other resources, as a danger to itself, or as both.

If the reason is competitive, is the shark defending a territory? Although this idea is frequently mentioned, it must be emphasized that territoriality in sharks is still only a theory, and has not been scientifically established. If gray reef sharks were territorial in the usual sense, one would expect that a resident would exclude other gray reef sharks with as much or more vigor than it would exclude other species. Behaviors such as threats and chases have never been observed between individual sharks, even though they are frequently close enough together for this to happen.

Individuals, in fact, intermix freely in both baited and unbaited situations with no obvious aggression toward one another. Is it possible that all the sharks at a particular spot recognize each other as familiar individuals? Would a shark from afar be recognized as a stranger and attacked? This would seem unlikely for the loosely-grouped sharks found on the outer reefs, considering the extent of their movements and the numbers of other sharks they must encounter. Trackings of these sharks tagged with ultrasonic transmitters show they can make location changes of up to 15 kilometers per day, and are less site-oriented than the sharks of the lagoon reefs. Territoriality in these sharks, therefore, is improbable.

Yet there are other observations which do suggest a type of territoriality, or at least a site-dependent dominance. Sometimes a lone shark on a lagoon pinnacle reef will swim directly up to a newly arrived diver and exhibit a mild or moderate threat display, without any apparent provocation by the person. If the diver (or sub) then advances on the shark, its threat intensifies and an attack can be easily induced (Figure 8). These lone sharks inhabiting the lagoon pinnacles or patch reefs are the most aggressive ones we have encountered at Enewetak. Is it possible that these individuals are in a "territorial phase," while others, such as those from the ocean-reef dropoff, are not? This question could probably be answered by a detailed telemetry study — tracking a number of neighboring sharks over periods of several months or more. One could then intercept and observe these sonically-tagged individuals at various times and places to look for signs of territorial behavior.

McNair believes that he has seen territorial behavior in certain gray reef sharks at Enewetak that he identified by scars or other markings. According to McNair, there is a "predictable difference in temperament when the same individual is encountered in different areas. On one piece of reef, the shark may always be aggressive, for example, while a half mile away it may be docile or shy, indicating that the first place was 'home.' After seeing this pattern repeat itself with the same individual several times, territoriality seems the only logical conclusion." Whether this indicates territoriality is a semantic question. Some would call an area of elevated aggressiveness or dominance a "dominion," unless actual forceful expulsion of intruders were demonstrated. Whatever it is called, site-dependent aggression in sharks would be a significant finding, and McNair's observations should be confirmed by more quantitative studies.

Another possibility is that the sharks are attacking because of a defensive, *antipredatory* motivation, regarding the sub as an object dangerous to themselves. If so, the exaggerated-swimming display has the same warning function as the rattling of a rattlesnake. And yet if this is the

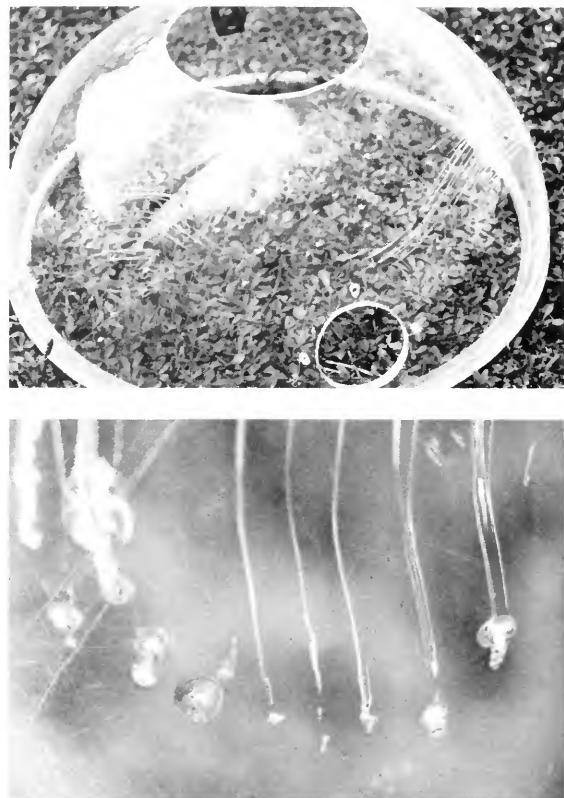


Figure 8. Acrylic dome of the Shark Observation Submersible showing several bite scars (tooth scratches) from attacks by gray reef sharks. (Photos by J. McKibben)

case, it is a real mystery why the sharks do not just swim away when pursued by the relatively slow-moving submarine. Is it possible they do not realize they can easily outswim the sub? The other common reef sharks (blackfin, whitetip, silvertip) always move away when chased, often in a high-speed burst, but the gray reef sharks more often choose to stand and fight. Behaviorists often refer to "flight distances" and "fight distances" in predator-prey situations, the latter delimiting what is sometimes called a "personal space" surrounding the animal. When a predator is seen approaching, the prey animal will flee when the predator reaches the flight distance. If, perhaps by surprise, the predator gets to within the fight distance, the prey may suddenly turn and attack. This attack presumably gives it a better chance for an eventual escape. In the case of the gray reef shark, there does not seem to be any flight distance; only the fight distance. The shark permits the submarine to approach without any real effort to get away. After attacking, however, the shark often flees the area at high speed.

If the antipredatory hypothesis is correct, then one must ask why the sharks need such a

behavior. What predators might represent a danger to the gray reef shark, itself a relatively large predator? Larger species do occur in the same areas, for example the tiger shark, *Galeocerdo cuvieri*, and the Galápagos shark, *Carcharhinus galapagensis*, but the extent of their predation on gray reef sharks is unknown.

What other possibilities are there for the unusual aggressiveness of the gray reef shark? Marine biologist Richard Johnson, in his book *Sharks of Polynesia*, argues that this species may be expressing a general *dominance*, such as for the purpose of intimidating potential competitors for food. He relates an incident from the Cook Islands in which a speared but escaped fish was about to be eaten by a moray eel. "A gray reef shark appeared and was observed to direct a display posture toward the eel, which persisted in its efforts to feed on the fish. The shark abruptly terminated the display and attacked the eel, leaving a noticeable white slash." In a potentially antipredatory context, he reports an observation in which a gray reef shark apparently displayed to an approaching hammerhead shark, *Sphyrna mokarran*, much larger than itself. Johnson suggests that exaggerated-swimming display occurs "under such a variety of circumstances, it seems no single motivation can adequately account for all situations."

Aggressive Behavior in Other Sharks

Besides gray reef sharks, do other species exhibit aggressive patterns such as threat, chase, or attack? Definitely yes, but for most sharks the information available is mainly anecdotal bits and pieces. Careful observational studies are needed, both in the natural environment and in captivity situations such as Myrberg and Gruber used to study bonnethead sharks. They noticed the similarity between the hunch posture of the bonnethead and the more conspicuous threat display of the gray reef shark. Both have similar postural elements — arched back, snout up, and pectoral fins down — but the exaggerated-swimming component was not seen in the bonnetheads. It was significant that the hunch, although only rarely seen, occurred mainly by resident sharks toward newcomers, or when a diver-observer entered the pool. A hunch posture also was noted in captive blacknose sharks, *Carcharhinus acronotus*, and in free-ranging silky sharks under related circumstances.

The bonnetheads also made "hits" on other individuals, especially newcomers. Similar hits were observed in scalloped hammerhead sharks, *Sphyrna lewini*, in the Gulf of California during studies of their schooling behavior by A. Peter Klimley and myself (see page 65). Are such hits aggressive, or for another reason, such as courtship? It is well known that mating in sharks can be rather rough on the females, as the frequently seen "mating scars" attest (Figure 9). Some such scars are

definitely tooth marks from bites, as on gray reef sharks, while others appear more like scrapes caused by hits with the snout, as on female hammerheads. These scars are believed the result of ardent courtship activities by males and/or efforts by males to gain purchase on females during copulation. Eugenie Clark, of the University of Maryland, observed courtship biting in the short-nosed gray reef shark, *Carcharhinus wheeleri*, in the Red Sea. Writing in the *National Geographic* magazine, she described how a female "swimming among a group of sharks would break away, almost as if inviting trouble. A male in the group would quickly oblige, rushing at her and biting her, often severely. Each would eventually return to the group." In one case, observed at a distance, a male appeared to make an attempt at copulation after biting the female. These "courtship attacks" produced quite deep gashes on the female's fins and pelvic flanks, which appeared to heal rather quickly. Damaging as they may be, however, such courtship bites are not considered aggression in the usual sense of the word. Bites on male sharks, however, may be a different matter.



Figure 9. Mating bites on a female gray reef shark from Enewetak. Note the severity of the tooth gashes, some of which were produced by bites using both jaws. (Photos by J. McKibben)

Recent evidence suggests that the mako shark, *Isurus oxyrinchus*, is a rather aggressive species (Figure 10). Robert Johnson and Jeffrey Landesman, of California State University, Long Beach, have observed interactions in baited aggregations of pelagic sharks off southern California and have noted how aggressive the mako appears in comparison to the more commonly seen blue shark, *Prionace glauca* (see page 42). In several instances, one mako was observed to chase another away from the bait basket, as if protecting a personal space or the food source itself. Open-mouthed "jaw-gapes" were frequently seen (perhaps a type of threat), and the sharks sometimes charged divers. Some males bore clear bite scars, possibly a sign of intraspecific fighting. Underwater photographers Howard Hall, Marty Synderman, and others have seen similar behaviors in baited makos and are unanimous in assessing their disposition toward divers as aggressive. Thus far, no mako shark has actually bitten a diver, but there have been some close calls, and the consensus is that if a mako is not treated with caution, a serious attack might occur.

Do any other sharks attack man for antipredatory or other non-feeding reasons? Both the Atlantic and Pacific species of lemon shark, *Negaprion brevirostris* and *N. acutidens*, have been reported to make violent retaliatory attacks on boats or divers if sufficiently provoked, such as by being speared or harpooned. Some attacks, however, occurred even with non-contact provocation. John Randall, in a chapter in *Sharks and Survival*, relates incidents in Florida in which lemon sharks charged and bit boats after being chased over shallow flats. According to Richard Johnson, the lemon shark in French Polynesia, while generally shy of divers, is "widely noted for its malevolence if disturbed. Attempting to touch, let alone prodding, shooting at, or spearing, is reported to result in an attack released in anger against the person or boat involved."

In none of the above lemon-shark incidents was a specific threat posture noticed, but an experiment by A. Peter Klimley, while a graduate student at the University of Miami, is significant. At the Sharkquarium, on Grassy Key, Florida, he dressed in a wet suit painted to resemble a killer whale (complete with dorsal fin) and entered an enclosure containing several lemon sharks. He swam in a "porpoising" manner at an eight-foot shark, and it immediately became agitated — swimming in front of him in rapid, tight circles and figure-eights and displaying repeated rapid openings and closings of the mouth. These behaviors appeared to be directed at Klimley, and were probably threats. They were not seen when Klimley swam at the sharks wearing a normal bathing suit.

The Great White Shark

What about aggression in the great white shark, *Carcharodon carcharias*, the world's largest predatory fish and close relative of the mako? Might some of the attacks by white sharks on humans be due to aggression, perhaps territorial, rather than to feeding? This intriguing idea has been repeatedly advanced, but on close examination has little support. For one thing, territorial residents usually confront and threaten intruders before resorting to attack. Most white-shark attacks have occurred without warning, from behind the victim, as if the shark were stalking prey. Furthermore, aggressive attacks — like those of the gray reef shark — are usually forceful, all-out efforts. According to Daniel Miller and Ralph Collier, who have recently published a well-documented analysis of shark attacks in California, most white shark attacks were "apparently slow, deliberate movements." They reached the general conclusion that "most of the attacks resemble the feeding behavior of an isolated, large shark that appears to be investigating an object." John McCosker, Director of San Francisco's Steinhart Aquarium, emphasizes that



Figure 10. The shortfin mako shark, *Isurus oxyrinchus*, aggressively approaches the photographer during a baiting session off Santa Catalina Island, California. (Photo by C. Matheson)

the great white shark is a "man-attacker but not a man-eater" and usually releases its human victim shortly after the first bite. He points out the similarity of a black neoprene-suited skin diver to the shark's normal pinniped prey (seals). Miller and Collier likewise mention how a person paddling on a surfboard could also resemble a pinniped from below. It seems most reasonable, therefore, that the white-shark bites are cases of mistaken-identity predation. Why do the sharks release their victims? Probably because they quickly sense that something is wrong — that the person (often wearing a neoprene suit, lead weights, and a steel tank) is not the food object they expected.

Does this imply that white sharks do not have aggressive behaviors? Not necessarily, for large bite scars have been seen on male whites, possibly the result of aggressive action by other whites. Fights between white sharks, of course, are presently conjecture, but some intraspecific interactions have been noted by Australian underwater photographers Ron and Valerie Taylor, who have filmed baited white sharks many times off southern Australia. Valerie writes that whites avoid being close together, and if two are on a collision course, "each, on sighting the other, will flick away at great speed." One large white they observed seemed to have an "unchallenged right of way," and smaller ones always gave way to it as soon as it was within sight. Although the Taylors never observed outright aggression between white sharks, they did witness a case in which a white was the recipient of aggression by a much smaller sea lion. In 10 or 15 minutes of active harassment, the sea lion succeeded in chasing the white shark from the area. In California, sea lions have been observed on several occasions to chase and nip at mako sharks, causing them to flee the area (J. Landesman, M. Synderman).

In conclusion, it is becoming clear that quite a few species of sharks participate in some aggressive interactions. Does this support Baldridge's suggestion that most shark attacks on man are non-feeding motivated? Perhaps, but more information is needed before this can be said with certainty. The gray reef shark remains the only shark presently known to attack man for violating a specific warning display. Is it unique in this regard? Probably not, but only future behavioral studies will tell. Unfortunately, most other species of dangerous sharks are more difficult to observe in the natural environment than is the gray reef shark.

Donald R. Nelson is a Professor of Biology at California State University, Long Beach. He has been studying sharks since 1962, when he was a graduate student at the University of Miami.

Acknowledgment

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Selected Readings

- Baldridge, H. D., Jr. 1974. *Shark Attack*, 236 pp. New York, NY: Berkley Medallion Books.
- Baldridge, H. D., Jr., and J. Williams. 1969. Shark attack: Feeding or fighting? *Military Medicine* 134: 130-133.
- Clark, E. 1981. Sharks — Magnificent and misunderstood. *National Geographic* 160(2): 138-187.
- Ellis, R. 1975. *The Book of Sharks*, 320 pp. New York, NY: Grosset and Dunlap.
- Gilbert, P. W., ed. 1963. *Sharks and Survival*, 578 pp. Boston: D. C. Heath and Co.
- Johnson, R. H. 1978. *Sharks of Polynesia*, 170 pp. Papeete, Tahiti: Editions du Pacifique.
- Johnson, R. H., and D. R. Nelson. 1973. Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. *Copeia* 1973: 76-84.
- Klimley, A. P. 1974. An inquiry into the causes of shark attacks. *Sea Frontiers* 20(2): 66-75.
- Klimley, A. P., and D. R. Nelson. 1981. Schooling of the scalloped hammerhead shark, *Sphyrna lewini*, in the Gulf of California. *Fishery Bulletin* 79(2): 356-360.
- McCosker, J. E. 1981. Great white shark. *Science* 81, 2(6): 42-51.
- McNair, R. 1975. Sharks I have known. *Skin Diver* 24(1): 52-57.
- Miller, D. J., and R. S. Collier. 1980. Shark attacks in California and Oregon, 1926-1979. *Calif. Fish and Game* 67(2): 76-104.
- Myrberg, A. A., Jr., and S. H. Gruber. 1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. *Copeia* 1974: 358-374.
- Nelson, D. R. 1977. On the field study of shark behavior. *American Zoologist* 17: 501-507.
- Nelson, D. R., and R. H. Johnson. 1980. Behavior of the reef sharks of Rangiroa, French Polynesia. *National Geographic Society Research Reports* 12: 479-499.
- Springer, S. 1967. Social organization of shark populations, pp. 149-174. In *Sharks, Skates, and Rays*, P. W. Gilbert, R. F. Mathewson, and D. P. Rall, eds., 624 pp. Baltimore: Johns Hopkins Press.
- Taylor, V., and R. Taylor, eds. 1978. *Great Shark Stories*, 403 pp. New York, NY: Bantam Books.

Attacks on Animals

Sharks have been known to attack and at times devour a wide variety of land animals, including dogs, cats, cattle, and horses. Race-horses have been attacked a number of times in Australia, where they are routinely exercised in the surf. And there is one story of a thirst-crazed elephant which, in 1959, stampeded into the sea off Kenya, evidently in search of water on a nearby island. It never made it; huge sharks attacked and tore the pachyderm to shreds.

Adapted from *Shark Attack*
by H. David Baldridge

Lemon Sharks: Supply-Side Economists of the Sea

by Samuel H. Gruber

Sharks comprise one of the most important and successful groups of top predators in the marine environment. In the pelagic realm, for example, ubiquitous sharks, such as the blue, dusky, silky, and oceanic whitetip, may represent the most numerous large predators in the sea. Yet the influence of these creatures on such factors as exchange of energy between trophic levels remains largely unknown. This is because very little is known of the basic biology of most sharks. Much of what is known arises from fishery statistics or experimental research. Few comprehensive field studies have been undertaken in which the ecology of a single species has been broadly investigated.

To bridge the gap in our understanding of the basic biology of sharks, a five-year, multidisciplinary study, supported by the National Science Foundation, has been undertaken to assess the role of the lemon shark, *Negaprion brevirostris*, in the tropical marine environment. The overall objective of this program is to provide a conceptual model for this species with which we will be able to predict its "cost of living" in units of energy, its rate of production, and, eventually, its impact on the animal communities on which it feeds. To make these predictions, we are studying a number of major biological variables, such as behavior, population dynamics, and bioenergetics.

Little is known about the actual effects of "apex predators," such as sharks, on the marine ecosystem. Indeed, little is known about the ecology of sharks in general. By way of contrast, the flow of solar energy to primary producers via photosynthesis is fairly well understood. How that energy in the form of living tissue gets transferred from trophic level to trophic level, however, is less understood. For example, at the apex of the food web, we have little idea how fast sharks grow, how long they live, how much food they require, how efficiently they convert food into tissue, and so on. In short, we do not know much about how these

higher predators make a living or where they acquire their resources.

Information on the dynamics of shark populations — including data on age, growth, food intake, and mortality — is required to develop a rational approach for managing this under-utilized living resource. Yet such statistics are simply not available because historically sharks have not been an important fishery resource in the United States. However, with the implementation of the 200-mile United States fishery conservation zone a few years ago, fishery management councils were mandated by federal law to provide management plans for the utilization of living resources, including the top predators. Results of the present research on the lemon shark can directly aid fishery scientists by providing baseline data for estimating rates of

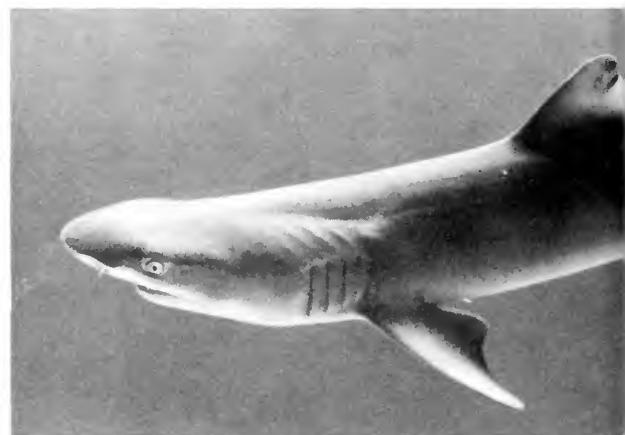


Photo by Ed Fisher

production in shark populations — the biological basis for any resource management.

The choice of the lemon shark as a subject for study came about after serious consideration. First, it is a highly successful species as judged by abundance within its range. It is a member of the most successful family of sharks and grows to large size. Possibly the most important aspect is this species' ability to adapt to captivity. Oceanaria are able to keep adults in large tanks for years; smaller lemon sharks have been kept under rigidly controlled conditions for periods of up to six years.

Field Studies

The actual research in our program can be broken down into a number of subtasks under the major headings of field and laboratory investigations. The first field study is an orthodox mark-and-recapture program. Nearly 1,300 young lemon sharks have already been tagged and released back into the environment. The eventual goal is to mark 2,500 of

these sharks over a period of five years. The recapture of about 10 percent of our marked population will permit us to estimate such variables as population size, growth rates, mortality of the various age groups, local movements, and long-term migration.

Each of the captured sharks has been weighed, measured, and catalogued as to sex. It was then fitted with a plastic tag in its dorsal fin and a dart tag was placed in its back behind the fin. Then it was given a freeze brand and a small plastic identification tag was surgically implanted in its body cavity. Finally, it was given a shot of tetracycline to mark it for age and growth determination. Tetracycline is taken up in the hard parts of the shark's body, such as the vertebral centra which make up its flexible spine. These

study on the effects of tagging on growth was done using 35 lemon sharks held under semi-natural conditions. The unmarked (control) sharks grew slightly faster (8 percent by weight) than the marked subjects. Thus the tagging method does seem to affect the shark.

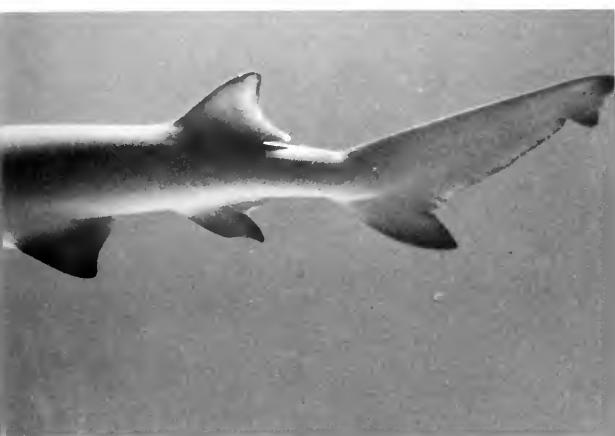
Another subtask is our ongoing investigation of lemon shark eating habits. We have identified a number of prey items from these sharks by pumping out their stomachs. Food items consist mostly of teleost and crustacean remains, including fish, crawfish, crabs, and, curiously, lots of turtle grass. Some larger lemon sharks specialize in stingrays as evidenced by the great number of spines embedded in their jaws and gums. However, more quantitative food studies presently under way must be completed before we can hope to understand the impact of lemon shark populations on the communities on which they feed.

In sum, an essentially pristine population of lemon sharks has been sampled, measured, and systematically marked. Resulting data are being integrated into the model of input/output energy relationships of this species. One final point is that we have begun an aerial census of lemon sharks. This method will give us an independent estimate of lemon shark abundance.

A second field study involves acoustic telemetry of the lemon shark. Little is known about shark behavior because sharks in general are wide-ranging animals. However, for the overall project to have meaning we must know what the animals do from day to day. This is especially true if we are to assess the relative importance of activity to their budgeting of energy in the natural environment. Thus we have placed transmitters on eight lemon sharks and have followed their movements for periods of up to 112 hours. We were able to pinpoint one shark's location every 15 minutes for five days.

Because lemon sharks frequently inhabit the shallow flats around mangrove islands, we were not able to track them with an ordinary boat and so we developed a very stable airboat. In addition to the airboat, we have employed a motorized glider to make aerial observations of shark behavior.

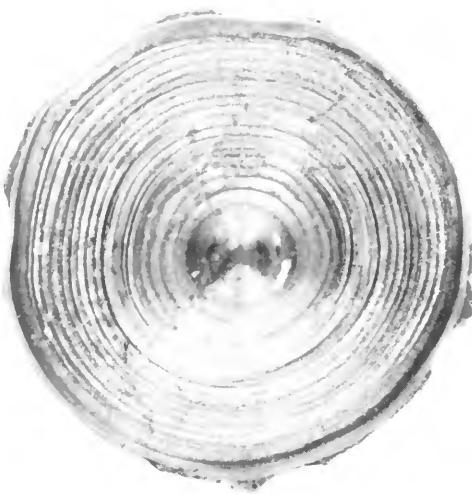
Several major points about the lemon shark's behavior can be inferred from the trackings. First, the larger sharks (1.8 to 2.2 meters in length) are somewhat site-oriented, although not as much so as the very young ones. We observed recurring patterns of activity in which certain of the lemon sharks returned to a spot just to the east of North Bimini, Bahamas, each day. We considered this area a refuge, and by aerial observation we confirmed the presence of several other lemon sharks milling about there. Unlike some other species, lemon sharks do not passively drift with the current. Measurements taken during tidal changes verified that the animals are able to orient with respect to a



A 62-centimeter (total length) lemon shark. This size is typical of the young specimens used in laboratory research. The lemon shark grows to a maximum size of more than 3 meters.

centra have rings in them in the same way that a cross section of a tree shows annual growth rings. The problem with sharks, especially tropical ones, is that we don't know how many rings are laid down per year. By injecting the animal with tetracycline, a fluorescent marker is made on the ring at the time of injection. If the animal is recaptured say five years later, there will be a ring that shows up under ultraviolet light and it will be a relatively simple matter of counting rings to determine the number of rings elaborated in unit time. Then it will be possible to fix the age of any lemon shark simply by counting the number of rings in a centrum.

Preliminary findings from this tagging study indicate that young lemon sharks remain localized in their first years of life. Also, they grow more slowly than had been previously thought. A control



Cross section of the vertebral centrum from a 2.34-meter lemon shark. The concentric rings are the key to determining a shark's age. Injected tetracycline accumulates on the outer ring and will show up under ultraviolet light when the shark is recaptured years later. (Photo by author)

particular locale and maintain a heading across or into the current.

Our lemon sharks were almost equally active day and night, with a rate of movement just over 1.5 kilometers per hour. However, this rate rose at dawn and dusk to nearly 2.5 kilometers per hour; this was because the lemon sharks were strongly affected by the sun. Each morning and evening they made a long, concerted move toward the sun. Thus we concluded that the lemon shark is crepuscular, a

finding which agrees with that of other marine biologists who have observed that reef sharks are also more active at twilight.

Still the belief persists that sharks are nocturnal — and there is good scientific evidence that, for some species, this is true. For the lemon shark, however, the evidence is conflicting: although our field studies did not reveal an increase in activity at night, our laboratory experiments clearly did. In a respirometer, both the rate of activity and the metabolic rate significantly increased at night. Perhaps size differences or effects of captivity can explain this disparity, but we will need more data before we can identify this shark's period of peak activity.

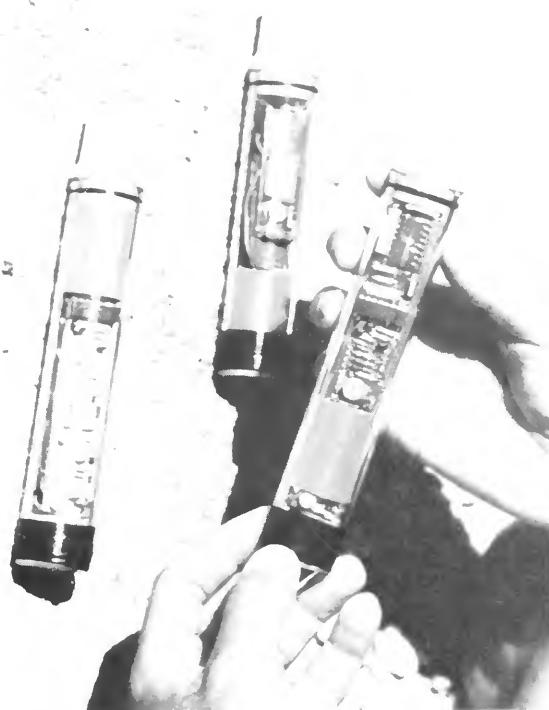
The underwater acoustic beacon attached to the shark is directional, so we were able to observe our tagged animals several times underwater. On five occasions, during three different trackings, the sharks were associated with several jack fish species. Because of the unusual interaction between the jacks and sharks we tentatively concluded that lemon sharks may utilize the expanded sensory capabilities of a school of jacks as an aid in finding prey.

While lemon sharks spend much time in the shallow flats, they are not restricted to that habitat. One large shark, which had been captured in waters only 1.5 meters deep, swam over a drop-off into 400 meters of water on the first day of tracking. The next morning we located it on a reef in about 20 meters of water. This was repeated a year later when a 2.5-meter male shark swam from a reef out into deep Gulf Stream waters and then moved 100 kilometers north before returning to the shallow reefs off Miami Beach.

The concept that emerges from this tracking and from other fishery data is that of an ever-expanding horizon for the lemon shark.



Underwater photograph of a transmitter being attached between the dorsal fins of a lemon shark. The cigar-sized transmitter is tied to a thin plastic plate, which is secured to the shark by two barbs imbedded in its flesh. This procedure takes less than five minutes if the shark is calm. (Photo by Dee Scarr)

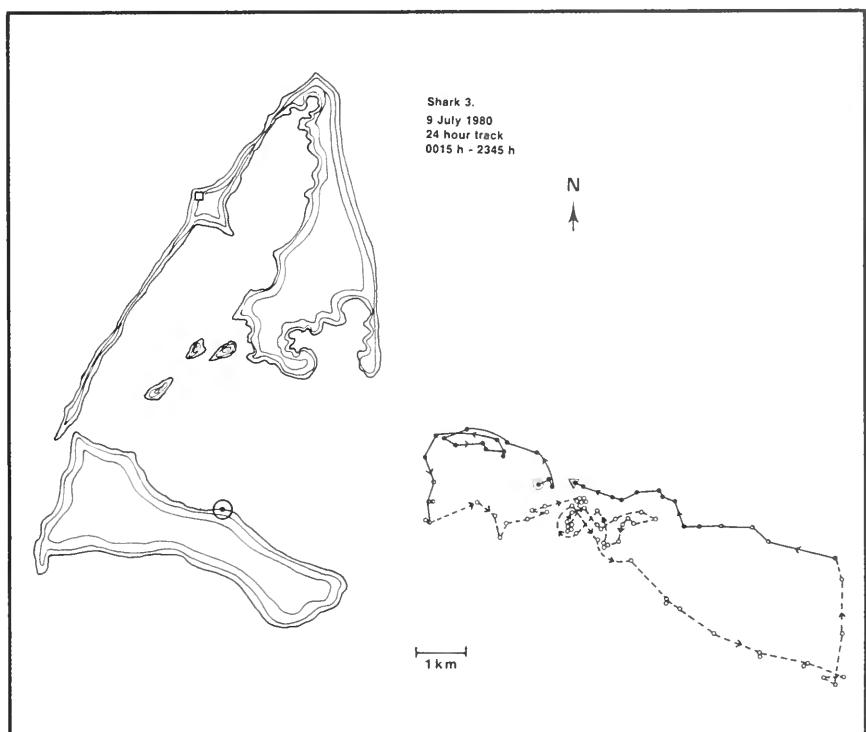


Three standard ultrasonic transmitters used to track sharks. Designed by Don Nelson, they emit a 40-kilohertz acoustic signal. (Photo by Don Nelson)



The ultralight powered glider used to track sharks from the air. Assembled and launched from the deck of a research vessel, it weighs 50 kilograms and folds into a package 5.5 meters by 1.75 meters. (Photo by Irene Brown)

Bimini Island, showing the movements, over a 24-hour period, of the third shark tracked by the research team. The small circles are fixes which were taken at regular intervals. The larger circle and arrowhead represent the beginning and end of this tracking, respectively. The solid line and filled circles represent nocturnal activity, while the dashes and open circles show this shark's path during the daylight hours. The map demonstrates that this shark made a long run east at sunrise and west at sunset. This pattern was repeated on five successive days. The area where the shark lingered and doubled back is a daytime place of refuge for lemon sharks.



During the first few years of life, the species remains restricted to a relatively small area, perhaps 6 to 8 square kilometers. As the shark nears maturity, it has gradually increased its activity space to about 300 square kilometers, but still it remains in the shallow flats and bays near land. After maturity, the shark expands its territory to include reefs and some deeper offshore waters. At this point, long migrations may be undertaken. Yet the shark remains attracted to the coastal zone; females bear their young in grass flats, lagoons, and other very shallow tropical habitats.

Laboratory Studies

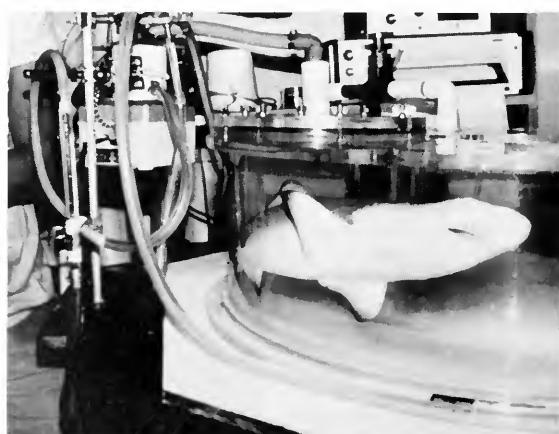
As for the laboratory part of our project, the primary objective involves balancing the "energy budget" for the lemon shark. In other words, we would like to be able to account for the fate of all calories the shark takes in. Although a shark receives its calories from the living tissue of its prey just as we do from our food, it partitions these calories in a somewhat different manner. For us, much of our caloric intake goes toward providing the heat necessary to keep our bodies warm. Lemon sharks, being cold-blooded, do not have this caloric "expense." However, they are at the mercy of the environmental temperature to keep up their bodily activities. This means that if the water temperature falls too low the shark could die of starvation because its activity rate is directly proportional to temperature. The major utilization of a shark's calories goes toward activity, while some energy is required to break down food into its useful components and run the biochemical and excretory machinery. The remainder is used in respiration and growth. By balancing the "energy budget" of the lemon shark, we will be able to specify the rate, amount, and sources of energy that this predator must remove from its environment to maintain itself at observed levels of activity and growth.

The laboratory investigations are organized into three areas: metabolic studies, blood gas parameters during exercise, and intake and production studies. The lynchpin of the laboratory work is metabolic rate. How much energy does the shark consume in its daily activities? What are the diel variations in caloric expenditures and what are the causes of such variation? What is the maximum sustained rate of caloric expenditure? How does the performance of the shark compare with its caloric utilization? To answer these questions, we have built a metabolic chamber in the form of a sealed circular raceway. A small shark placed in the chamber is free to move about unhindered. The difference between the (saturated) oxygen content of water entering and that of water leaving the tank is a measure of the instantaneous oxygen consumption of the shark. Since oxygen uptake can be converted into calories burned, this method is called indirect calorimetry, and is a well-known

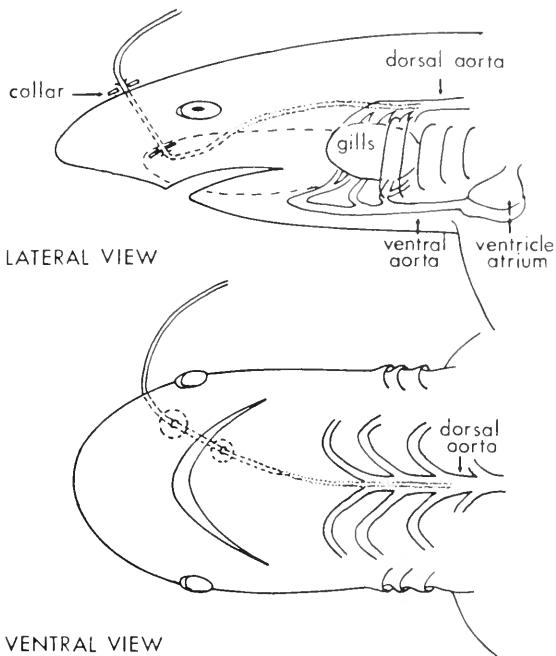
technique for measuring metabolism of aquatic organisms. By manipulating the subject sharks prior to or during testing, it is possible to answer basic questions about metabolism. For example, if we wish to determine the energetic cost of digesting a meal rich in fats, we simply compare the metabolism of a shark under standard conditions to that of a shark just fed an oily mackerel.

To date, we have established that the average metabolic rate of the young lemon shark is about 200 milligrams of oxygen consumed per kilogram of shark per hour. This works out to about 1.2 kilocalories burned every hour. However, that rate increases at night and decreases during the day. The tropical lemon shark is thus about two times more metabolically active than its temperate cousin, the spiny dogfish. Lemon sharks have the ability to "rest" on the bottom, but, curiously, they burn about 9 percent more energy resting than when swimming. This is probably because the resting shark must actively pump water over its gills—an energy-consuming process—and because oxygen extraction may be inefficient at low water velocity.

To determine extraction efficiency and to understand the kinetics of the oxygen flow from environment to shark, we have developed a surgical technique for implanting a fine tube in the dorsal aorta, a major blood vessel serving the shark's body. The surgery is rapid and recovery is complete, often within three hours. Sharks that have been operated on usually eat the same day, and the tubes have remained in place for more than 80 days. With this tube we can withdraw a sample of shark blood at will and rapidly analyze its pH, electrolyte, and gas composition. This study has produced some striking and unexpected findings.



A respiration chamber used to measure the oxygen consumption and thus the metabolic rate of young lemon sharks. Containing 70 liters of circulating seawater, the donut-shaped chamber provides enough space for a 60-centimeter shark to swim nearly four body lengths in circumnavigation. (Photo by Peter Bushnell)



VENTRAL VIEW

Through a surgically-implanted tube, researchers can withdraw a sample of blood from a shark at will, directly from the animal's aorta. This sketch shows the position of the plastic tubing, which is inserted under the skin of the buccal cavity and worked back until blood signals that it has entered the aorta. The tube is then passed through the head and fixed in place with two plastic buttons (collar). Sharks have survived up to 80 days with this tube in place.

Oxygen-Rich Blood

The circulatory system of the lemon shark is unlike that of any other fish thus far studied. During exercise, most fish and mammals draw on the oxygen reserves of their venous blood. For example, during a chase, the partial pressure of oxygen bound in the blood flowing through a fish's veins may fall to a half of the resting value. Lemon sharks, however, do not have a venous reserve. Under normal conditions, they draw off most of the blood-bound oxygen on the arterial side of the circulatory system leaving almost no oxygen in venous blood.

However, like other predators, lemon sharks must chase down prey and flee predators. To do so, they have evolved a different strategy. During exercise, they produce an abundance of red blood cells which quickly enter their bloodstream. Simultaneously they open an extra 20 percent of their gill surface to permit enhanced oxygen exchange. Finally, the blood itself has a great affinity for oxygen, completely saturating at a partial pressure some 200 percent lower than most fishes.

Similar high-affinity blood has been found in burrowing animals and fetuses, which inhabit

environments with a low oxygen content. Thus we suggest that this respiratory mechanism is an adaptation for survival in an oxygen-poor habitat. This makes sense, since lemon sharks are often found in areas with low oxygen concentrations, such as very shallow backwater bays within mangrove islands, where organic matter accumulates and water temperature can exceed 30 degrees Celsius.

The remaining laboratory studies are centered on rates of production in the lemon shark and include experiments on food intake, digestion, assimilation, and growth. One often hears the statement that the shark is the perfect "eating machine." This conjures up the image of a mindless automaton always on the prowl, mechanically attacking and devouring anything that gets in its way. This impression has even been supported in some scientific literature: one worker stated that hunger and satiation play no role in the behavior of a shark. Common sense would dictate that a vertebrate animal as highly evolved as a shark would have mechanisms to control and synchronize food intake, which, of course, they do. Curators in oceanaria and scientists using sharks as subjects have long known that, within limits, sharks will not overeat; and they can be quite fussy about what they ingest.

So, to establish the roles of hunger and satiation, the rate and rhythms of food intake, the efficiency of food conversion into growth, and the rate of growth itself, we placed a number of sharks into several large aquaria (up to 6,000 liters) and carefully controlled water quality factors, such as temperature, salinity, oxygen content, and illumination. These sharks were given unlimited amounts of preweighed fish fillet and allowed to feed to satiation twice per day for 100 days. Results clearly demonstrated that hunger waxes and wanes on a four-day cycle. The average shark (70 centimeters long) consumed an equivalent of 3 percent of its body weight daily. By the end of the 100-day trial, it had grown in weight by 50 percent. This means the shark converted 19 percent of its ration to growth. The remainder, some 43.3 kilocalories, was "burned" daily as fuel to run the shark's physiological machinery. Thus the picture emerges of an animal that feeds in bouts and controls its intake within narrow limits, growing at a rate similar to other young predators, such as the freshwater pike.

The second stage in the processing of food occurs in the stomach. We have therefore measured rates of digestion and gastric evacuation as estimators of meal size, feeding rates, and feeding frequency. Rate of digestion could limit the number of meals per week, while stomach volume might set a limit on prey size. Of course, digestion provides the only source of energy available to the animal and, as such, must be specified to estimate



A lemon shark breaks the surface to grab a preweighed piece of fish fillet. Each shark in this 100-day experiment was allowed to eat as much as it wanted, twice a day. (Photo by author)

the animal's daily energy requirements. By withholding food for three days, then feeding sharks a ration of fish fillet equal to 3 percent of their bodyweights, then pumping stomachs at 3-hour intervals, we determined that digestion was nearly complete after only 24 hours. Using dyed fish, we found that food can pass completely through the shark's digestive tract in only 12 to 14 hours. However, dyed feces continues to show up for two to three days. Feeding sharks live fish equivalent to 20 percent of their body weights gave a very different result. We have recovered undigested food from the stomach even after 48 hours. Thus meal size is an important factor in rate of digestion and, ultimately, in feeding frequency.

Growth Rate Studies

The final and one of the most important parameters of an "energy budget" is growth rate, which is a direct measure of production. The rate at which an organism removes energy from a lower trophic level defines its impact on the ecosystem and establishes, at least in part, the dynamics of trophic webs. Since growth in a top predator represents the "end of the line" for the transfer of energy up the food web, it would be possible to deduce the overall efficiency of that transfer if production rate, population numbers, and type of food were all known. Thus we have studied growth in some detail.

The growth of sharks is poorly understood. Some species, like the Japanese smooth dogfish,



A fish inside a fish. This X-ray of a lemon shark shows the whole pinfish, *Lagodon rhomboides*, that it ate one hour earlier. Digestion appeared complete after approximately two days.

reach maturity in only two years. Others, like the great white shark, may require a decade or more to attain a length at maturity of 4 meters. The growth rate of the lemon shark is probably between these extremes. Originally, it was thought that this species reached maturity (2.4 meters) in only 12 months. Later that figure was revised upward to 24 months. Based on these tentative conclusions, the lemon shark has become known as a rapidly-growing subtropical shark. However, my studies indicate a much slower rate of growth.

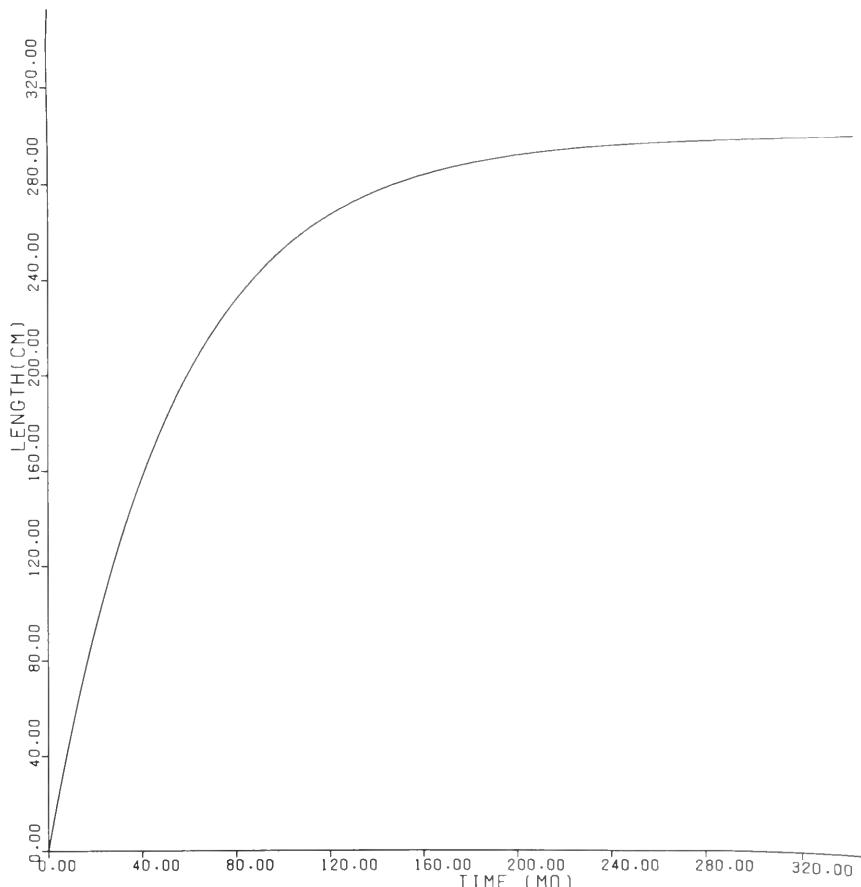
In Florida Bay, lemon sharks give birth in the spring to between four and nine young, each about 60 centimeters long. At first, these newborn lemon sharks rapidly increase in size, but growth decelerates over time until it reaches an asymptote. We have measured the rapid growth of these newborns in two experiments. In both studies, the sharks were free to consume as much food as they wanted.

The growth rate of these 40 experimental animals averaged about 0.6 millimeters per day. Such a rate implies that 7.5 years are required to reach maturity, provided that growth is constant. If this figure is correct, the lemon shark grows

considerably slower than first suggested. Support for this contention was gained when we ran a simple computer simulation of growth, assuming length at birth of 60 centimeters, maturity at 245 centimeters, and a maximum size of 300 centimeters. Again, assuming a gestation period of one year, maturity would be reached in just over seven years.

Besides revising our growth rate estimate for the lemon shark, these studies clearly show that food is a limiting factor. Captive lemon sharks grow four times faster than tagged ones. It is here that an analogy with supply-side economics applies. Crudely stated, supply-side economists suggest that by increasing the supply of economic products, demand for these products will automatically follow. Thus the economy can be manipulated and perhaps controlled.

In "biological economics," the same thinking applies. Clearly, without adequate supplies (that is, prey), predators cannot survive. Many examples of "boom and bust" situations are known in animal populations where the fate of a predatory species is directly tied to its prey. In our shark studies, we also find that productivity is dependent upon resources. In other words, if you



A computer simulation growth curve for the lemon shark, based on a gestation period of 12 months, a 60-centimeter birth length, and a 300-centimeter maximum length. Assuming the lemon shark reaches maturity (the beginning of sexual activity) at 245 centimeters, it would take some seven years to reach this length. This is close to the estimate of 6.5 years, which is based on laboratory studies and tagging returns.

increase the supply side of the system by providing more food, the demand will automatically rise and sharks will increase their intake, to a point.

Unfortunately, it is the opposite which usually occurs in nature these days. In the realm of the lemon shark, man has reduced environmental quality through pollution, construction dredging, commercial fishing, and other human activities. Thus the supply side of the shark's economy has been unfavorably affected. While I can only speculate that the numbers of lemon sharks have been declining in recent years, they could quickly get in trouble if their birth and growth rates were to fall. Lemon sharks have a reproductive strategy and growth similar to whales: low fecundity, slow growth, and delayed maturity. Thus, unlike most fish, shark populations can quickly become seriously depleted at the hands of man if care is not taken in their management.

Our research project is just over two years old; results seem to me like pieces of a jigsaw puzzle. Some of the pieces are partly formed while others are missing. Certainly, we will not find all the pieces (our program will run at least through 1983), but there will be enough so that an attempt can be made to come up with a representation of the life-style of the lemon shark to use as a basis for comparisons with other species.

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Suggested Reading

- von Bertalanffy, L. 1960. Principles of a theory of growth. In *Fundamental Aspects of Normal and Malignant Growth*, ed. W. W. Nowinsky, pp. 137-259. Amsterdam: Elsevier.
- Brett, J. R., and J. M. Blackburn. 1978. Metabolic rate and energy expenditure in the spiny dogfish, *Squalus acanthias*. *J. Fish Res. Bd. Canada* 35: 816-821.
- Gruber, S. H. 1980. Keeping sharks in captivity. *J. Aquaculture* 1(1): 6-14.
- Gruber, S. H., and A. A. Myrberg, Jr. 1977. Approaches to the study of the behavior of sharks. *American Zool.* 17: 471-486.
- Hobson, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. *Bureau of Spt. Fish. Wildl. Res. Rpt.* 73: 1-92.
- Holden, M. J. 1977. Elasmobranchs. In *Fish Population Dynamics*, ed. J. A. Gulland, pp. 187-215. London: John Wiley and Sons.
- Kleiber, M. 1975. *The Fire of Life: An Introduction to Animal Energetics*. Huntington, N.Y.: R. E. Krieger.
- Myrberg, A. A., Jr., and S. H. Gruber. 1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. *Copeia* 1974: 358-374.
- Nelson, D. 1974. Ultrasonic telemetry of shark behavior. *Nav. Res. Rev.* 27(12): 1-21.
- Olson, A. M. 1954. Biology, migration, and growth rate of the school shark (*Galeorhinus australis* Macleay) in southeastern Australian waters. *Aust. J. Mar. Freshwater Res.* 5: 353-410.
- Ricker, W. W. 1975. Computation and interpretation of biological statistics from fish populations. *Bull. Fish Res. Bd. Canada* 191: 1-382.
- Soucie, G. 1976. Consider the shark. *Audubon* 78(5): 36-54.
- Springer, S. 1950. Natural history notes of the lemon shark, *Negaprion brevirostris*. *Texas J. Science* 2(3): 349-359.
- Winberg, G. 1956. Rate of metabolism and food requirements of fishes. *Fish Res. Bd. Canada Transl. Series* 194: 1-202.
- Zahuranec, B. J. 1975. Shark research. Present status and future direction. ONR report ACR-208. Arlington, Va.

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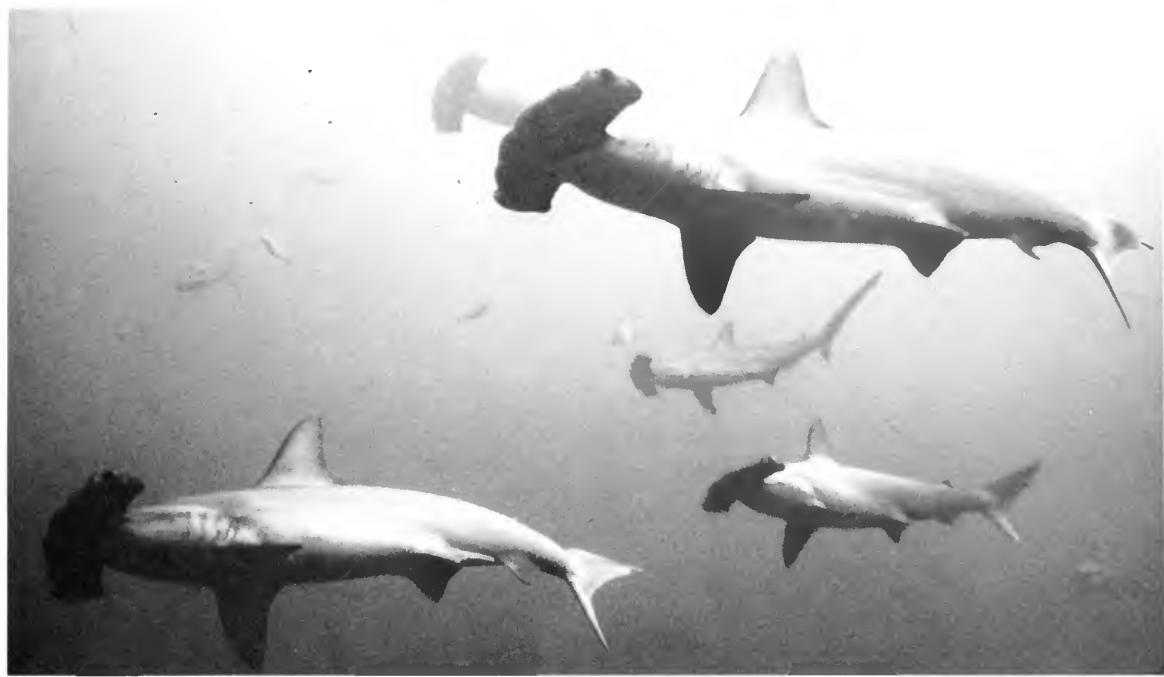


Photo by Marty Snyderman

Grouping Behavior in the Scalloped Hammerhead

by A. Peter Klimley

Although swimmers and sport divers usually encounter no more than a few sharks at a time, occasionally they sight a massive group of sharks concentrated in a small area. A number of such startling encounters in June of 1977 along the coast of the Gulf of Mexico near Corpus Christi, Texas, involved as many as 2,000 sharks concentrated in the surf zone along a 24-kilometer stretch of shoreline popular with bathers. This leads one to wonder how common grouping is among the more than 300 species of sharks. What types of sharks form such groups, and what behaviors go on within them? Are the groups composed of adult males and females engaging in courtship, adult females giving birth to their young, or juveniles seeking protection from predation? The common function of defense is less likely because of the paucity of predators large enough to feed upon sharks.

Fishery scientists and commercial fishermen have been aware for years of grouping, from variations in their catches. Sometimes numerous

sharks are caught on hooks on only one section of a longline, or are tangled in only one part of a gill net. Also, one longline and net haul may contain an enormous number of sharks; another may contain none. Some behavioral scientists have been fortunate enough to directly observe grouping on some occasions, more commonly from the deck of a ship or through the window of an airplane, however, than underwater in the shark's habitat.

Diversity of Grouping Species

Grouping (a gathering of three or more sharks) occurs in a wide variety of shark species with different evolutionary histories, habitats, and feeding habits. It occurs in the bullhead shark, *Heterodontus portusjacksoni*, considered primitive because of its possession of characteristics present in early fossil sharks. This shark spends its life inshore on a rocky bottom and feeds on invertebrates. The less primitive requiem (Carcharhinidae) sharks also group.

The blacktip *Carcharhinus limbatus*, the dusky shark *C. obscurus*, the sandbar shark *C. plumbeus*, and the gray reef shark *C. amblyrhynchos* also live inshore but are found more often in midwater and are primarily fish eaters. The basking shark, *Cetorhinus maximus*, and the whale shark, *Rhincodon typus*, both reported to group at times, generally live offshore and feed upon macroplankton. The scalloped hammerhead, *Sphyrna lewini*, spends most of the day along the dropoff region and moves offshore at night. It feeds on both offshore and inshore fishes and squid. In all, grouping has been reported in the scientific literature for five of the eight orders of sharks and has been observed in another, leaving only the hexanchiformes and pristiophoriformes orders without schooling members. Such diversity argues that grouping probably occurs in some part of the life cycle in most species of sharks.

Despite the large number of shark species observed to group, there has been little study of these groups or of the motivation behind sharks gathering in such groups. Observers have failed to determine whether such groups were aggregations with sharks responding to ecological factors, such as the presence of clumped prey or upwardly flowing currents, or were schools with members drawn together by social bonds. In addition, observers have failed to note whether sharks were swimming in a polarized or non-polarized school. Members of a polarized school all move together in a common direction, maintaining a constant distance from each other and changing their directions synchronously. Authors have referred to such groups as "large concentrations," "groups," "schools," and "packs"; only recently did Donald Nelson and Richard Johnson, both of California State University, refer to groups of gray reef sharks as "social groups."

So far, few attempts have been made at describing the size and sex of sharks actually within groups, as well as their behavior patterns. During the last four years, I have been studying by direct observation groups of three species of sharks, the leopard shark, *Triakis semifasciata*, the blue shark, *Prionace glauca*, and the scalloped hammerhead, *Sphyrna lewini*. Since my observations of groups of scalloped hammerheads are at this time the most complete, I will confine myself to this species in the rest of the article.

The Scalloped Hammerhead

Scalloped hammerheads spend most of the day along coastal and insular dropoffs and leave these sites at night, probably to forage in the surrounding pelagic environment. Three locations in the Gulf of California where the scalloped hammerhead schools regularly gather are at Isla Las Animas, El

Bajo (a seamount), and Las Arenitas, on the northwestern coast of Isla Cerralvo (Figure 1).

Scalloped hammerheads are ideal for underwater study because group members remain together, swimming near the surface in a relatively small area for prolonged periods during the day. They also are not aggressive at this time, and are not frightened by the repeated approach of investigators. A single hardship demanded of observers is that they must free-dive without the use of scuba tanks because the sharks rapidly move away from scuba divers, presumably responding to the sonically and visually conspicuous air bubbles emitted from their gear.

The members of scalloped hammerhead schools swim in a polarized fashion (Figure 2). The degree to which the sharks are oriented in a common direction is comparable to several other schooling bony fishes. Tanya Tarshis, an undergraduate student, found the mean angular deviation in the direction of individual sharks from a common direction of the group was 23.4 degrees. She calculated this by summing the deviations by vector addition. Although this measure of schooling has been determined for only a few species, the deviation is similar to that of a common schooler in southern California waters, a topsmelt, *Atherinops*. The mean three-dimensional distance between nearest hammerhead neighbors of 0.92 body lengths is less than that of the topsmelt and other marine schoolers, a silverside, *Menidia*, and the bonito *Sarda*, and a freshwater schooler, *Tilapia*. Although not yet measured, there appears to be an obvious tendency of members within the schools to follow directional changes of sharks along the front of the school.

In addition to swimming in a polarized fashion, the scalloped hammerheads form schools, not aggregations. They remain together at the locations because of an attraction to each other, not solely to an environmental factor, such as the presence of upward-lifting currents near the sloping ridge of the El Bajo seamount. When the current velocity at the seamount diminishes during slack tide, school members remain together, although their parallel orientation is generally less pronounced. While some prey species are occasionally observed in the vicinity of the seamount, the majority are in deeper waters offshore, yet the sharks remain near the seamount during the day.

Description of Groups

The average size of groups encountered during our free dives is about 20 sharks. However, groups with more than 100 sharks are not uncommon. The members of the schools are predominately female. During the summer of 1979, females outnumbered males by the ratios of 1.6 to 1 at Isla Cerralvo, 3.8 to 1

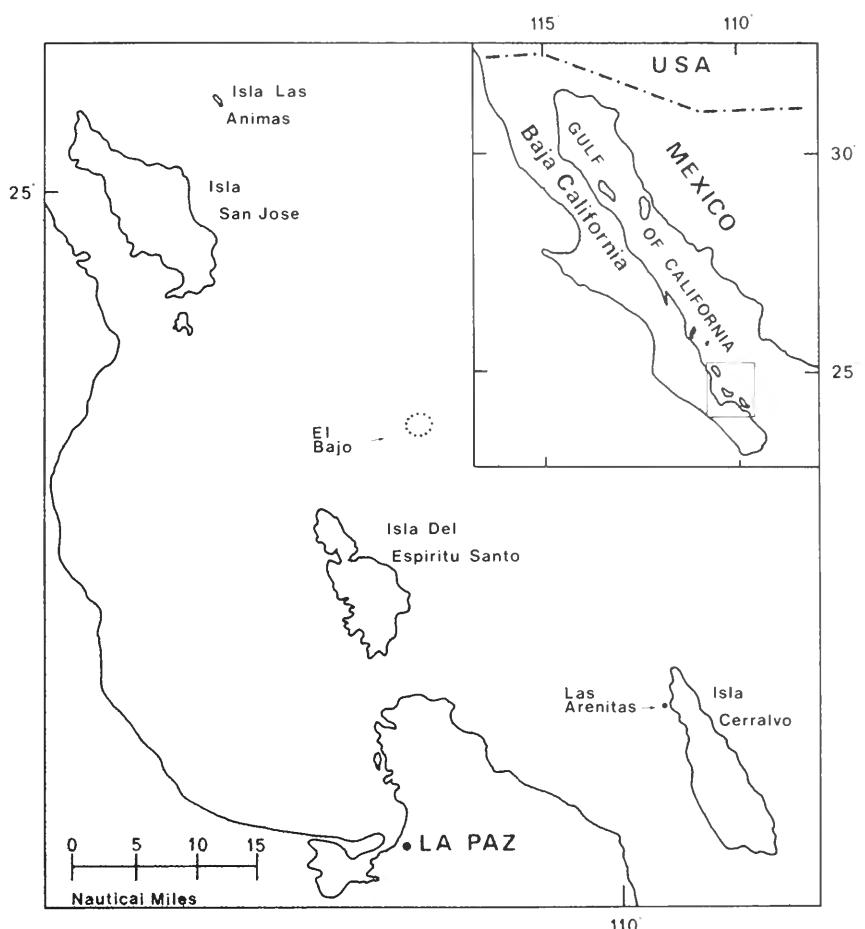


Figure 1. Three locations in the Gulf of California where schools of scalloped hammerheads have been repeatedly encountered: 1) Las Arenitas, a cluster of rocks 100 meters off of Isla Cerralvo; 2) El Bajo, a broad-surfaced seamount with its approximate extent marked by a dotted line; and 3) Isla Las Animas. (From Klimley and Nelson, Fishery Bulletin)



Figure 2. Hammerhead school as viewed from the side. Note polarized aspect of school with members oriented in the same direction and similarly spaced. (From Klimley and Nelson, Fishery Bulletin)

at the El Bajo seamount, and 3.1 to 1 farther north at Isla Las Animas. The sizes of sharks within the groups vary at different locations. Sharks from El Bajo Gorda, another seamount off the southern end of the Baja peninsula, were considerably larger, with median length of 196 centimeters, than those at El Bajo and Las Animas with median lengths of 176 and 161 centimeters, respectively. However, considerably smaller sharks moved into the El Bajo Gorda area during the spring of 1981.

The predominance of females appears to match previous fishery studies in which the catches of sphyrid and related carcharhinid species were strongly female-dominated. Similar disparities in sex ratios led fishery biologist Stewart Springer to examine numerous pregnant sandbar sharks to determine the sex ratio of their full-term pups. He also examined catches of newly born sharks. The parity in such ratios led him to hypothesize sexual segregation for the sandbar shark. He felt that adult males lived over a larger geographical and depth range, perhaps in deep, cool oceanic waters inaccessible to fishermen's gear, while the females were in warmer inshore waters accessible to fishermen. Because the temperature gradient between inshore and offshore waters lessens in late spring and early summer, he believed the males moved inshore then to mate with the females.

Measurements of the lengths of sharks swimming in the schools as well as their individual distances from each other were determined in the sharks' habitat using a photogrammetric technique known as stereophotography. I swam down to the edge of the school and positioned a beam with two separated cameras of parallel optical alignment facing toward a single or several sharks. I then depressed a trigger, simultaneously firing both cameras. Later, I measured under a microscope the minute distance between the snout and tail on the shark's photographic image (Figure 3b: l) and the separation between a point, either the snout or tail tip, on the shark's images from the right-hand and left-hand cameras (Figure 3b: $x_2 - x_1$). This displacement is equivalent to the 50-centimeter separation of the cameras and provides a scale with which to measure the shark's length from its image length (l) with a correction for imperfect camera alignment. The scalloped hammerhead in Figure 3 is the largest measured to date, reaching 371 centimeters. The shark's huge size should be evident to the viewer from the number of displacement lengths that will fit into the length of the shark image.

The promising stereophotographic technique will be used again in an attempt to verify our impression that larger sharks remain along the edges of the groups. From photographs taken from outside the group, one can measure approximate distances from the group's nearest edge to any shark within, and then compare the lengths of

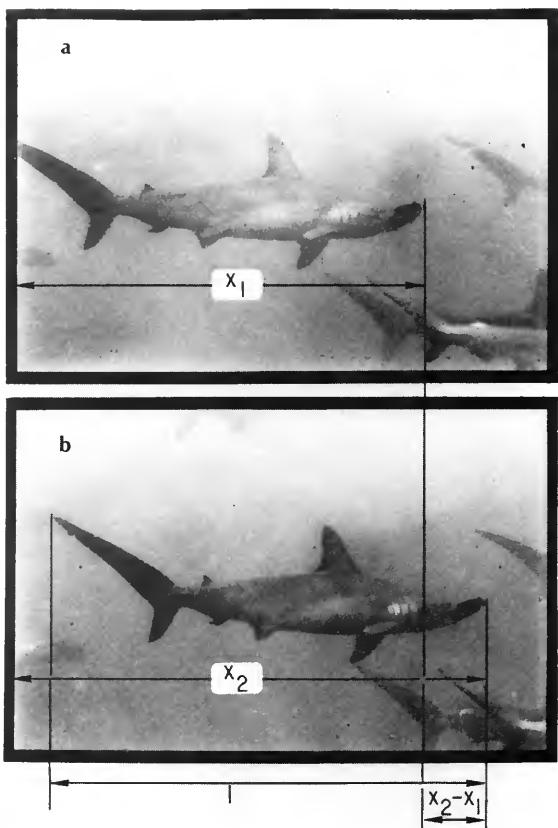


Figure 3. Stereophotographic pairs of a free-swimming hammerhead shark. Upper photograph (a) was taken by right-hand camera; lower photograph (b) by left-hand camera. Measurements of x_1 and x_2 were made with respect to the left-hand edge of the frame and resulted in the displacement ($x_2 - x_1$). Measurement l was made from the tip of the snout to the tip of the caudal fin. (From Klimley and Brown, CIBCASIO Transactions, in press)

peripherally located sharks to those centrally located.

Acrobatic Behavior

Hammerheads within the schools do not always maintain their parallel schooling orientation. Frequently single or several adjacent sharks accelerate from their parallel positions into acrobatic behavioral patterns. Commonly sharks tilt their bodies laterally, revealing their highly reflective undersides for prolonged periods of time. They then often accelerate upward or downward and shake their anterior torso or head spasmodically. The upper right-hand shark in Figure 4 is shown with its head thrust to the side during a headshaking behavior. This photograph was taken from a single 16-millimeter frame of movie film. There appear to be many variations to the behavior.

A shark may shake its head continuously, discontinuously, to one side, or to both sides. Sometimes the behavior involves just the head; sometimes the whole forward torso is thrust to the side. Earl Herald, the late director of San Francisco's Steinhart Aquarium, observed this behavior in hammerheads during one of his visits to Isla Las Animas and called it the "shimmy dance."

Most acrobatic of all behaviors is what I term "corkscrewing," which involves an explosive acceleration of the shark into a small circular path less than a body length in diameter while the shark rapidly twists its torso around 360 degrees. This all takes only a second. Almost as spectacular is a behavior pattern in which the shark quickly rolls onto its back and propels itself forward in a jerky manner with exaggerated beats of the tail, while at times thrusting its midsection to the side.

The three behaviors so far discussed all result in a reflection of light off the ventral surface of the shark, visible to the observer and to other sharks at a great distance. It is quite possible that these pulsed flashes of light are visual signals aimed at other members of the group. I am now measuring components of these frequently repeated behaviors and applying a statistical analysis to their spatial and temporal features to assess the extent of their stereotypy or constancy of form, which is an indicator that they are used in communication.

Other less-frequent behaviors occur within the groups. One is a sudden movement of a shark downward, hitting its snout against the back of the shark below. On two occasions sharks have ended "corkscrewing" behavior by contacting a nearby shark on its back. Another prominent behavior is a wide opening of the jaws. Within the group, this behavior is presumably directed at school

members, but at other times it is performed by solitary sharks in the sole presence of a diver. In this context it is probably a mild aggressive threat directed at the diver.

Although I have compiled a relatively complete catalog of behavior patterns in the last three years by direct observation and repeated viewing of extensive videotape samples, I am just beginning to see sequential relationships between the behaviors. The demonstration of a progression of behaviors characteristically occurring within the groups leading to responses, such as copulation, prey capture, or the attack of another shark, could lead to an understanding of the reason or reasons for grouping. Although behaviors such as "corkscrewing" have been observed to precede a "hit," which in turn released "headshaking" and momentary departure of the two sharks from the school in possible pairing behavior, the sequences have not been observed to lead to very revealing acts, such as copulation. Future research will center on further identifying serial relationships and on identifying behaviors outside the group by following one shark at a time, since the sequence-ending behaviors may be occurring in slightly deeper water away from the groups.

It is possible that some of the behaviors we have described may lead to mating. Many of the school members bear abrasions (see tagged shark in lower right-hand corner of Figure 4). These are small, recently inflicted, white contusions, where most of the dermal denticles are removed, or older, partially healed, black contusions (Figure 5). As one can see in the histograms, scars occur almost exclusively on females. Furthermore, these scars do not occur all over the females but primarily in the first three 10-percent-length-divisions on the right and left lateral and dorsal aspects. The predominance of scars on larger females and their restricted placement coupled with observations of the "hit" behavior suggest that these scars may be similar to other bite scars inflicted by other species of sharks during mating.

Function of Grouping

What then is the function of these massive groups of hammerheads? Four broad functional possibilities are likely: 1) reproduction — grouping to carry out courtship activities, 2) defense — grouping to avoid predation, 3) swimming efficiency — grouping for hydrodynamic advantage, and 4) feeding — grouping to increase predatory success through cooperation in locating or capturing prey, or the clumping of individuals centrally in relation to prey distribution.

Evidence points toward a rejection of the first hypothesis. A large number of the sharks are quite small, less than 140 centimeters long. Current examination of the reproductive systems of similarly sized sharks that were captured by local



Figure 4. Shark in upper right-hand corner performing head-shaking behavior. Note scarring and color-coded streamer tag on shark beneath head-shaking shark. (From Klimley and Nelson, *Fishery Bulletin*)

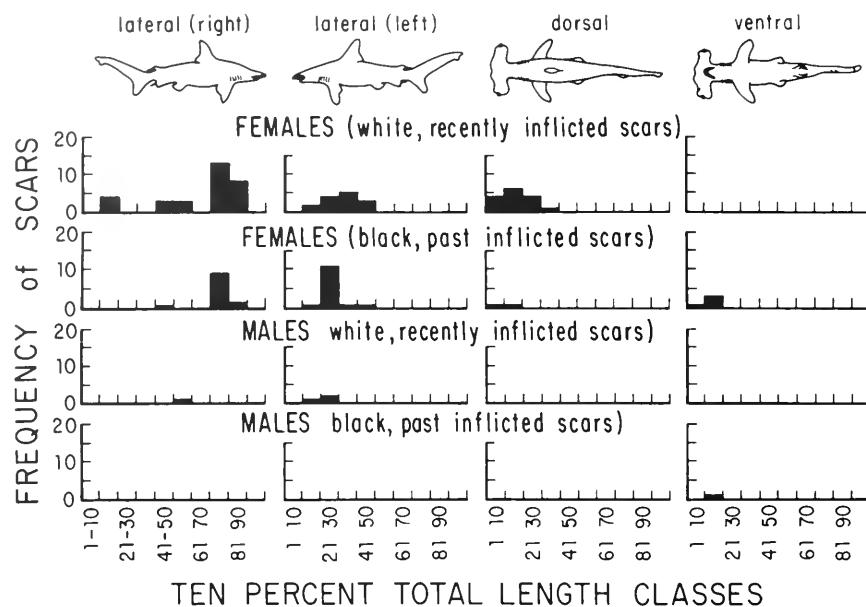


Figure 5. Frequency of recent and past-inflicted scars occurring within 10 percent divisions of the total length for different aspects of free-swimming male and female scalloped hammerheads. The scars were recorded from films taken at El Bajo during July and August, 1979. (From Klimek and Brown, CIBCASIO Transactions, in press)

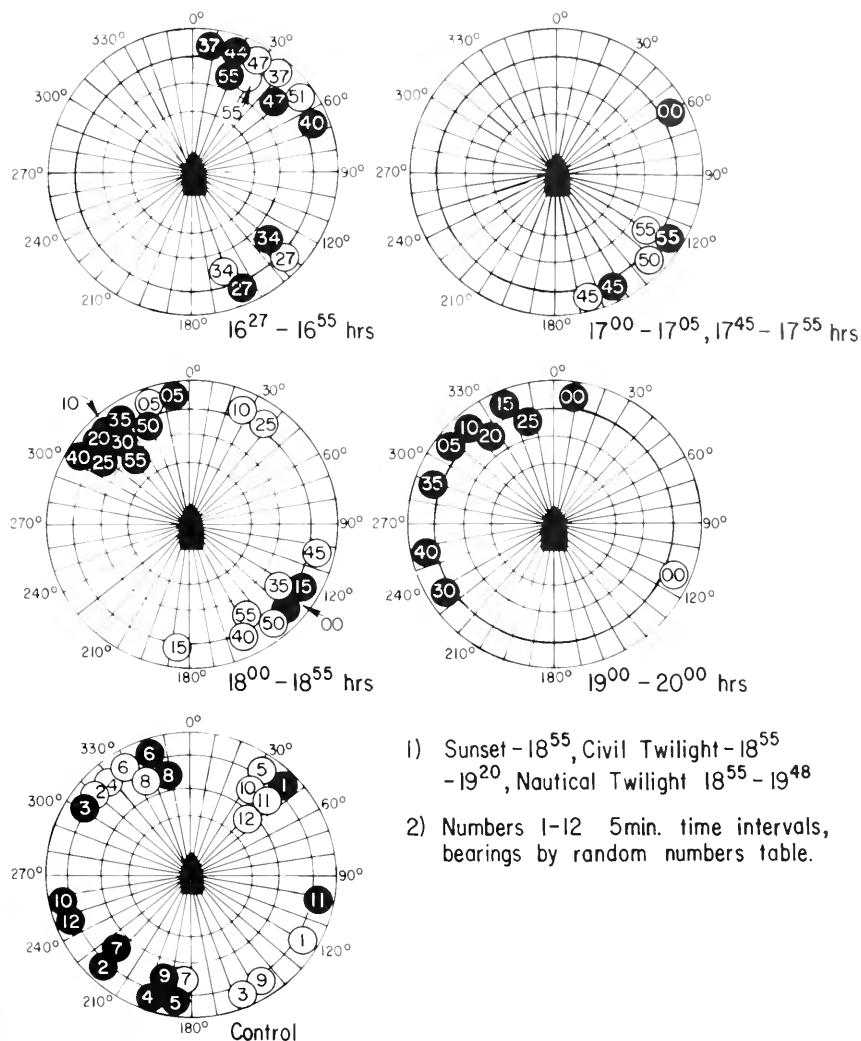
fishermen indicates these sharks are immature. Evidence for the rejection of the second hypothesis is the absence of any predators, such as the tiger shark, *Galeocerdo cuvieri*, or the white shark, *Carcharodon carcharias*, in the hammerheads' offshore habitats during the daytime when the hammerheads are swimming in schools. The third reason seems unlikely since the sharks remain near the upward-sloping seamount pinnacles even during slack tide, when currents are absent.

This leads us to the feeding hypothesis. Daytime feeding does not occur, or is an extremely rare event. Co-workers and myself have never witnessed what we have all agreed to be an unequivocal predatory act. Furthermore, several attempts at attracting members from the schools to macerated prey or to sounds resembling those generated by prey have only attracted five hammerheads.

Feeding must then occur during the night. Do the sharks move off the seamount at night in groups and stalk their prey cooperatively at that time? We have some evidence that the sharks leave the seamount at different times and in different directions, moving independently of each other. Nelson (see page 45) attached a telemetry transmitter to a school member (shaded circles, Figure 6). We then located the group, using this tagged shark, and attached another transmitter to a second shark (clear circles, Figure 6). In Figure 6 our first paired tracking is diagramed. After tagging the second shark we anchored the small tracking boat over the seamount pinnacle and took directional bearings on the two sharks at 5-minute intervals. More recent trackings, involving two tracking boats, have more precisely located the sharks.

Each polar plot in the figure can be thought of as a compass rose superimposed upon the boat's position, and the small circles represent the bearings of each shark with the exact times of these bearings within the circles. The first four polar plots refer to the four hours that the sharks were directionally positioned prior to their departure from the seamount area. It is evident that bearings of the two sharks (represented by the shaded and clear circles) during the first two hours were similar; look at the circles for 16:27, 16:47, 17:45, and 17:55. After 18:05 the sharks separated, one remaining northwest of the boat, the other remaining southeast of the seamount for a while before departing at 19:00. The second shark left the vicinity of the boat at 19:55. These departures and subsequent ones have occurred almost always at sunset. A comparison of the first four polar plots with the fifth control plot enables one to see that during the afternoon the compass bearings of the two sharks were not random but generally together. These and subsequent results are still inconclusive, since there is always the possibility that the sharks are separating in small groups and we have not yet been lucky enough, in the several paired trackings, to pick two sharks who moved off together.

Even if the sharks were not to forage socially, there could be an energetic advantage for the sharks to remain based centrally among nearby prey clumps. Such an advantage would occur if the clumps of prey were to exist in the surrounding epipelagic and mesopelagic waters. If these clumps were to be spread out over a large area, and the sharks were to move over greater distances, this energetic benefit would be lost. This reasoning has been used to explain colonial nesting in avian species.



- 1) Sunset - 18⁵⁵, Civil Twilight - 18⁵⁵ - 19²⁰, Nautical Twilight 18⁵⁵ - 19⁴⁸
- 2) Numbers 1-12 5min. time intervals, bearings by random numbers table.

Figure 6. Directional bearings at 5-minute intervals of two scalloped hammerheads tagged on 4 August 1980 at El Bajo at 13:35 (shaded circles) and 15:10 (clear circles). Time intervals noted within circles.

As the reader can ascertain, our knowledge of the ethology and behavioral ecology of the scalloped hammerhead is still too rudimentary to determine unequivocally the function of its massive schools. However, most certainly this species provides us with an ideal behavioral system to ask this type of question, and should lead to further insight into shark grouping as well as to a better understanding of the social behavior and means of communication of sharks. Perhaps we will find that sharks are not only supremely adapted to locate and capture their prey but also possess a varied social repertoire of behaviors that contributes to their evolutionary success.

A. Peter Klimley is in the graduate program at the Scripps Institution of Oceanography, La Jolla, California, where he is conducting research on the scalloped hammerhead, leopard, and blue sharks.

Recommended Reading

- Clark, E. 1963. Massive aggregations of large rays and sharks in and near Sarasota, Florida. *Zoologica*, 48: 61-64.
 Clarke, T. A. 1971. The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. *Pacific Science*, 25(2): 133-144.
 Gruber, S. H., and A. A. Myrberg, Jr. 1977. Approaches to the study of the behavior of sharks. *American Zoologist*, 17: 471-486.
 Klimley, A. P., and D. R. Nelson. 1981. Schooling of hammerhead sharks *Sphyrna lewini*, in the Gulf of California. *Fisheries Bulletin*, 79(2): 356-360.
 Klimley, A. P., and S. T. Brown. 1981. Stereo-photographic technique for the determination of lengths of free-swimming scalloped hammerheads, *Sphyrna lewini*, in the Gulf of California. *CIBCASIO Transactions*, in press.
 Myrberg, A. A., Jr., and S. H. Gruber. 1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. *Copeia*, 1974(2): 358-374.
 Nelson, D. R., and R. H. Johnson. 1980. Behavior of the reef sharks of Rangiroa, French Polynesia. *National Geographic Society Reports*, 12: 479-499.
 Parker, F. R., Jr., and C. M. Bailey. 1979. Massive aggregations of elasmobranchs near Mustang and Padre Islands, Texas. *Texas Journal of Science*, 31(3): 255-266.
 Springer, S. 1967. Social organization of shark populations, pp. 149-174. In *Sharks, Skates, and Rays*, eds. P. W. Gilbert, R. F. Mathewson, and D. P. Rall, 624 pp. Baltimore: Johns Hopkins Press.

Shark Repellents: Perspectives for the Future

by Samuel H. Gruber

Sharks attack men—and, less frequently, women—about 100 times each year. Probably many more incidents go unreported, but even so, shark attack must be considered a very rare phenomenon. Why, then, does the search for a truly effective shark repellent continue? First, there is a special helpless horror created by the thought of being attacked and bitten by a huge shark. The fear created by an attack is often blown out of proportion, and this in turn can affect the wider population by bringing such activities as recreational swimming or underwater salvage to a halt. Second, under certain conditions like marine or aviation disasters, the probability of shark attack can increase from vanishingly small to almost certain. The wartime accounts of attacks on shipwrecked sailors on the high seas attest to this, and such accounts can dramatically affect the morale of an entire fleet. Finally, sharks attack and destroy very expensive oceanographic instruments with some regularity. Not only is the equipment lost, but cruises are cancelled and programs can be delayed for months or even years. Thus the search for a repellent continues.

Haphazard Effort

Early investigations were done on a somewhat haphazard basis. A "shotgun" approach was used in hopes of stumbling upon some potent chemical substance which repelled sharks. In parallel work, various devices were developed to behaviorally disrupt or physically damage sharks. Attempts to fence popular bathing areas in Australia and South Africa were temporarily successful, but were eventually foiled by corrosion, tides, and shifting sands. Those two countries still make use of staggered gill nets, which catch and kill many sharks just beyond the surf at some bathing beaches. There have been some successful experiments with electrified barriers, but these are expensive to maintain and, like some electrical gadgets on the market, can be dangerous to divers. The "shark screen," a plastic sack that fills with water and hangs from the surface by a flotation ring, can prevent a shark below from seeing or smelling the person inside. For divers, the powerhead, or "bang-stick," can kill an attacking shark with an exploding charge to the head. However, as with the CO₂ dart, which is only disabling when fired into the shark's abdomen,

if you miss you may have one angry shark on your hands. An Australian has patented an underwater transmitter that mimics the call of the killer whale, a predator of sharks. Finally, there is a promising, light-weight chain-mail diving suit that shark teeth apparently cannot penetrate.

Yet none of these efforts has produced an entirely satisfactory repellent. The failure of the U.S. Navy's "Shark Chaser" underscores this fact. Shark Chaser is the best known, most widely used shark repellent ever produced. It was developed in a crash program during World War II in an effort to protect our servicemen. The work consisted of exposing captive smooth dogfish, *Mustelus canis*, to a number of systemic poisons and other toxic agents. Scientists scored the effect of each substance on feeding responses of the dogfish and found that rotten shark flesh inhibited feeding better than any of the toxic agents. Chemical analysis suggested that copper acetate might mimic the rotten flesh and that a dense, black-water soluble material—nigrosine dye—might hide the swimmer from sharks. Thus thousands of cakes of those compounds were fabricated and eventually distributed to GIs. Actually, some of the field tests were very encouraging. But in the end, Shark



Valerie Taylor being bitten by blue shark while testing light-weight chain-mail diving suit. (Photo by Jeremiah S. Sullivan)

Chaser dispersed rapidly in the open sea and did not always chase sharks. In the middle 1970s, the military dropped it.

Today, the outlook for developing an effective chemical shark repellent is better. The Office of Naval Research supported studies on shark biology for 15 years in hopes of understanding shark behavior and sensory physiology. These studies are about to pay off. Development of a repellent will require the testing of many substances on live sharks. Techniques previously developed in Navy-supported basic research are now available to scientists so that more valid bioassays can be undertaken.

What, then, characterizes a chemical shark repellent? First, the substance or stimulus must interrupt a special, coordinated behavior — the attack. Contrary to popular belief, many or perhaps most attacks are motivated by factors other than hunger. The implication is that a stimulus which merely inhibits feeding may not be adequate in all cases. Therefore, any definition of repellency must go beyond interruption of the feeding drive alone. Since its effect must be instantaneous, a repellent should work at the level of the sensory receptors. Systemic poisons or neurotoxins, for example, are too slow to be useful. So, an adequate repellent must provide an aversive stimulus field sufficient to induce a highly motivated shark to turn and leave the area regardless of the source of motivation. Finally, for practicality, the repellent should be quite stable for a long shelf-life, relatively inexpensive, effective in minute amounts, and harmless to man.

Modern Repellent Research

In the 1970s, research on shark repellents shifted from basic shark biology to the search for biologically effective natural marine products. In theory, a marine organism may have "invented" an effective shark repellent during the process of evolving a protective mechanism against predation. Many thousands of toxic and noxious fishes and invertebrates are known, and more remain to be discovered. However, the most thoroughly studied and promising of these protected forms is a small Red Sea fish, the Moses sole, *Pardachirus marmoratus*. Research by Dr. Eugenie Clark of the University of Maryland established that the Moses sole produces a proteinaceous, slowly-dispersing, toxic secretion that protects it from shark attack. The status of this and other research on shark repellents was summarized in January, 1981, at a symposium sponsored by the American Association for the Advancement of Science (AAAS). Topics ranged from the structure and function of pardaxin, the purified active toxin of the Moses sole; to the behavior of sharks when exposed to pardaxin; to the types of toxic organisms found in the world's oceans.



Powerhead for shark defense. (Photo by Jeremiah S. Sullivan)

Three possible lines of future research emerged from this meeting. First, a group led by Israeli Dr. Naftali Primor suggested continued study of pardaxin so that its physiological mode and site of action on sharks could be unambiguously specified. Primor favors the theory that the gill membranes are the target organs for pardaxin, which shuts down the "sodium pump" by interfering with production of the enzyme adenosine triphosphatase. This in effect short-circuits the shark's electrochemical gradient and makes the gill "leaky" to water and ions. Urea and sodium flow from the shark's plasma through the gills and into the sea. Other ions enter the gills from the surrounding seawater. Thus, the shark's osmoregulatory and salt-balance systems are disrupted. According to Primor, these ionic fluxes could be responsible for the observed repellent effect of pardaxin.

Another group of Israeli scientists, led by Dr. Elihau Zlotkin, has taken a somewhat different approach. Zlotkin recognized the surfactant and detergent-like qualities of pardaxin and, in a series of experiments, demonstrated that: 1) pardaxin reduces the surface tension of water by 60 percent and foams in aqueous solution; 2) the amino acid sequence of pardaxin's N-terminal is extremely hydrophobic and positively charged, which would amplify its interaction with phospholipid (cell) membranes; and 3) depending on dosage, pardaxin can completely disrupt synthetic phospholipid membranes or, in lower concentration, interfere with membrane physiology such as specific ion channels or membrane cable properties. Zlotkin realized that the complicated sequence of 162 amino acids of which pardaxin is composed could not be synthesized except perhaps by genetic engineering techniques. Additionally, pardaxin is an unstable compound, which can only be stored in a freeze-dried form that is 70 percent less effective than the fresh secretion. He thus suggested that it might be worthwhile to investigate industrial

surfactants, theorizing that these strong detergents might act much like pardaxin in repelling sharks.

The third group, represented by Drs. Gerald Backus and Doug McClure of the University of Southern California, called for continued testing of a wide variety of naturally occurring toxic compounds so that their potentials as shark repellents could be scored and catalogued.

There is one common element in all three lines of research: study of the behavior of live sharks under controlled conditions. This is where I could perhaps contribute, since I had been studying shark behavior in the laboratory for many years. At the January AAAS meeting Zlotkin and I decided to test his theory (that simple, inexpensive detergents might repel sharks). Under a small grant from the Office of Naval Research, Zlotkin traveled to Miami with eight substances, including perhaps 90 percent of the world's supply of freeze-dried Moses sole extract — some 27 grams.

Testing Surfactants

The first task was to develop test methods for screening these eight substances. We settled on three bioassays. The first was a simple lethality test. We seined about 200 pupfish, *Fundulus heterocleitus*, from a muddy shore near the Rosenstiel School of Marine and Atmospheric Science in Miami. The fish were placed individually in small containers and exposed to various concentrations of the eight test substances. We found that one of the surfactants was more lethal by an order of magnitude than the Moses sole extract. A second detergent-like surfactant was equally as lethal as the extract; at 10 parts per million, it killed pupfish in six hours or less. The other test substances were mildly toxic or completely benign. These findings encouraged us to move on to the shark tests. We used 41 lemon sharks, *Negaprion brevirostris*, in the studies. These were all young sharks up to 4 kilograms in weight and under three years old. Some of the sharks had been in captivity for up to two years, but most had been held for no more than 10 weeks.

The first test was a simple feeding trial in which food was withheld from 15 sharks for two days. Then a bait was prepared by attaching a

25-cubic-centimeter syringe to a whole blue runner, *Caranx cryos* (Figure 1). The syringe was fitted with a plastic tube which protruded out the bait's mouth. It was possible for the experimenter to manipulate the bait in such a way that the shark grabbed the blue runner's head in its mouth. At that instant the contents of the syringe were released into the mouth of the attacking shark (Figure 2). The outcome of these trials took one of three forms: 1) the shark, unaffected by the substance, continued its attack, tearing off and consuming the bait's head; 2) the shark was mildly affected but continued to feed or, more frequently, did not press the attack; and 3) the shark was obviously and strongly repelled, and dashed away disoriented. Some time later, a shark in this third category would show signs of distress, including labored breathing and color changes.

Results of these tests showed that the same detergent that killed pupfish in low concentration, a common compound found in industrial cleaning agents, was 10 times more effective at repelling sharks than was the Moses sole extract. A second surfactant was as effective as the extract, and two others were mildly repellent. Four of the test substances did not deter hungry sharks from feeding. From these tests, we concluded that Zlotkin was correct: certain industrial surfactants mimic the action of pardaxin. Additionally, the repellent effect of the Red Sea sole is probably universal and not dependent upon the shark having prior experience with the toxic fish. We reach this conclusion because the Moses sole is restricted to the Red Sea yet our lemon and nurse (*Ginglymostoma cirratum*) sharks are repelled by pardaxin. Two other Atlantic species, the spiny dogfish, *Squalus acanthias*, and the Atlantic sharpnose shark, *Rhizoprionodon* sp., were shown in other laboratories to be affected by pardaxin.

Because feeding trials depend on the motivational state of the shark we were limited in the number of tests that could run on a single day. For example, after feeding, and especially after exposure to a toxin, our sharks typically lost interest in the bait for a couple of days. We therefore decided to develop a second bioassay which was more-or-less independent of the shark's motivation.



Figure 1. Feeding bioassay: a 20-centimeter-long blue runner, *Caranx cryos*, is prepared as a bait by attaching a 25-centimeter syringe to the fish. The plastic tube extends out the bait's mouth. (Photo by author)



Figure 2. Feeding bioassay: an 80-centimeter-long lemon shark, *Negaprion brevirostris*, attacks the bait and grasps the head in its mouth. Simultaneously the experimenter releases the test substance into the shark's mouth. (Photo by E. Zlotkin)

Tonic Immobility Tests

The response we selected is based on a behavior known as catalepsy or tonic immobility. If a shark (or other species, from primate to insect) is disoriented by being held in an inverted position, it will fall into a relaxed, trance-like state (Figure 3). This state can last for 30 minutes or more, during which the shark is quite insensitive to stimulation. For example, it is possible to perform minor surgery under tonic immobility.

We felt that tonic immobility might offer a rapid and repeatable way to screen large numbers of activating compounds. A test would consist of tonically immobilizing a shark, then instilling a known concentration of a substance into the shark's mouth (Figure 4). The test would be scored as positive if the shark "awoke" by flipping over and righting itself (Figure 5). Because of the control over dosage, the ability to give repeated trials, and the unambiguous behavioral end-point, we expected to produce some precise threshold values for the eight test substances. Our expectations were verified. The tonic immobility trials proved to be a rapid and reliable way to compare surfactants. Again, the same potent surfactant effective in the first two assays was found to be four times more effective than the Moses sole extract at terminating tonic immobility and 30 to 100 times more effective than its nearest surfactant competitor. Thus the three bioassays—lethality, feeding, and tonic immobility—gave essentially the same result.

This work has shown that it is possible to use live sharks as subjects in behavioral bioassay trials. This means that it will be possible to screen a large number of compounds in a relatively short time. The work also confirmed Zlotkin's hypothesis that cheap, readily available industrial surfactants will repel sharks. This opens up a number of

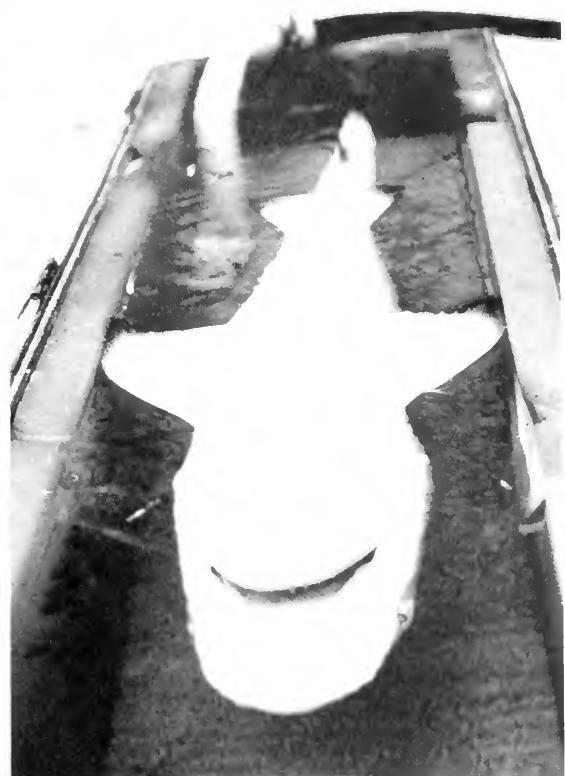


Figure 3. An 85-centimeter lemon shark inverted and under tonic immobility. A shark will remain essentially immobile for at least 10 minutes except for breathing movements of the mouth and gills. (Photo by author)



Figure 4. Tonic immobility bioassay: experimenter releases a test substance into the immobilized shark's mouth. (Photo by author)



Figure 5. Tonic immobility bioassay: a shark "awakens" from tonic immobility after a test substance has been released into its mouth. (Photo by author)

possibilities for repellent research, since we now have a theoretical framework to guide our experiments and some reliable tests to answer our research questions. Zlotkin and I plan to continue this work with the dual goals of producing (isolating or synthesizing) a highly effective chemical repellent based on industrial surfactants and elucidating the repellent's physiological mode of action.

After the laboratory studies are complete, field testing must be undertaken. This requires a completely different technology, including ultrasonic telemetry and activity monitoring devices. If the field tests are positive, the ultimate tests involving wild sharks and human subjects must be performed. Along with these, the problem of packaging the repellent for rapid deployment must be solved. Although our research may someday be applied to the manufacture of a mass-marketed repellent for bathers, our first priority is to protect Navy divers and underwater military hardware.

Thus much work remains before a final product will become widely available. Still, there is renewed enthusiasm in the research community and renewed interest at the funding agencies. Interaction of these two factors has a way of producing results. Prospects for the long-term solution to the shark repellent problem seem more favorable today than ever before.

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Selected Reading

- Baldridge, D., and J. Williams. 1969. Shark attack: feeding or fighting. *Military Med.* 34: 130-133.
- Clark, E., and S. Chao. 1973. A toxic secretion from the Red Sea flatfish *Pardachirus marmoratus* (Lacepede). *Bull. Sea. Fish. Res. Sta. (Haifa)* 60: 53-56.
- Gruber, S. 1980. Keeping sharks in captivity. *J. Aquaricult.* 1: 6-14.
- Gruber, S., and A. Myrberg. 1977. Approaches to the study of the behavior of sharks. *Amer. Zool.* 17: 471-486.
- Primor, N., and E. Zlotkin. 1975. On the ichthyotoxic and haemolytic action of the skin secretion of the flatfish *Pardachirus marmoratus* (Soleidae). *Toxicon* 13: 183-187.
- Tuve, R. L. 1947. Technology of the U.S. Navy "Shark Chaser." *Naval Instit. Proc.* 73: 522-527.



Photo by Elgin Ciampi,
National Audubon Society

Advice to Swimmers, Divers, and Victims

Always swim with a companion, and do not wander away from a coherent group of other bathers and thereby isolate yourself as a prime target for attack.

Do not swim in water known to be frequented by dangerous sharks. Leave the water if sharks have been recently sighted or thought to be in the area.

Although not conclusively proven, human blood is highly suspect as an attractant and excitant for sharks. Keep out of the water if possessed of open wounds or sores. Women should avoid swimming in the sea during menstrual periods.

It is not always convenient, but very murky or turbid water of limited underwater visibility should be avoided if possible. In any event, a particularly watchful eye should be maintained for shadows and movements in the water. If there is any doubt, get out at once.

Refrain from swimming far from shore where encountering a shark becomes more probable.

Avoid swimming alongside channels or drop-offs to deeper water which provide ready access for a shark.

Leave the water if fish are noticed in unusual numbers or behaving in an erratic manner.

Take no comfort in the sighting of porpoises, for this does not at all mean sharks are not about.

Avoid uneven tanning of the skin prior to bathing in the sea, for sharks apparently respond to such discontinuities of shading.

Use discretion in terms of putting human waste into the water.

Avoid swimming with an animal such as a dog or a horse, etc.

Take time to look around carefully before jumping or diving into the sea from a boat.

Particularly at low tide, take notice of a nearby offshore sandbar or reef that might have entrapped a shark.

Avoid swimming at dusk or at night when many species of sharks are known to be searching for food.

It just might be a good idea to select other than extremely bright colors for swimwear.

Never, in any form or fashion, molest a shark no matter how small it is or how harmless it might appear.

Keep a wary eye out towards the open sea for anything suggestive of an approaching shark.

Advice to Divers

Never dive alone. Not only might the very presence of your diving buddy deter the shark, but together you have a far better chance of becoming aware of a nearby shark in time to take effective countermeasures. Furthermore, if something did happen to you, at least there would be assistance close at hand.

Do not in any way provoke even a small shark — not by spearing, riding, hanging on to its tail, or anything else that might seem like a good idea at the time. Even a very small shark can inflict serious, possibly fatal, injury to a man.

Do not keep captured fish, dead or alive, about your person or tethered to you on a stringer or similar device. Remove all speared or otherwise wounded fish from the water immediately.

Do not spearfish in the same waters for such extended periods of time that curious sharks may be drawn to the area by either your prolonged quick movements or an accumulation of body juices from numbers of wounded fish.

Leave the water as soon as possible after sighting a shark of reasonable size, even if it appears to be minding its own business. Submerged divers, as opposed to surface swimmers, have a better chance of seeing a shark making investigatory passes prior to being committed to attack. Use smooth swimming strokes, making no undue commotion, in reaching the safety of a boat or the shore. To the greatest extent possible, remain submerged where chances are greater for watching the shark and countering its charge if attack occurs. Do not count on the shark either circling or passing close at hand without contact before it makes a direct run.

Use discretion in the choice of wetsuit colors in terms of conditions and sea life prevalent in the waters of intended operations. Do not take a chance on being mistaken for the area's natural prey of choice.

Carry a shark billy or plan to use the butt of a speargun for this purpose if necessary. Such devices have been shown to be very effective in holding an aggressive shark at bay until its ardor cools.

Take full advantage of your submerged position and limits of visibility to be aware always of nearby movements and presences. Shark attack case histories indicate that such vigilance has played a major role in lowering injuries and mortality rates among diver-victims.

Do not maneuver a shark into a trapped position between yourself and any obstacle such as the beach, reef, sandbar, or possibly even a boat.

As with swimmers, do not wander away from an established group of other divers and possibly give thereby an appearance of fair game. Avoid diving at dusk and at night.

Advice to Victims

Try to remain calm and take full advantage of weapons available to you.

Use any object at hand to fend off the shark while at the same time not intentionally provoking it further.

Keep fully in mind the limitations of such devices as powerheads, gas-guns, spearguns, etc., and do not expect them to accomplish the impossible. Such weapons, if used improperly, may serve only to further agitate the shark.

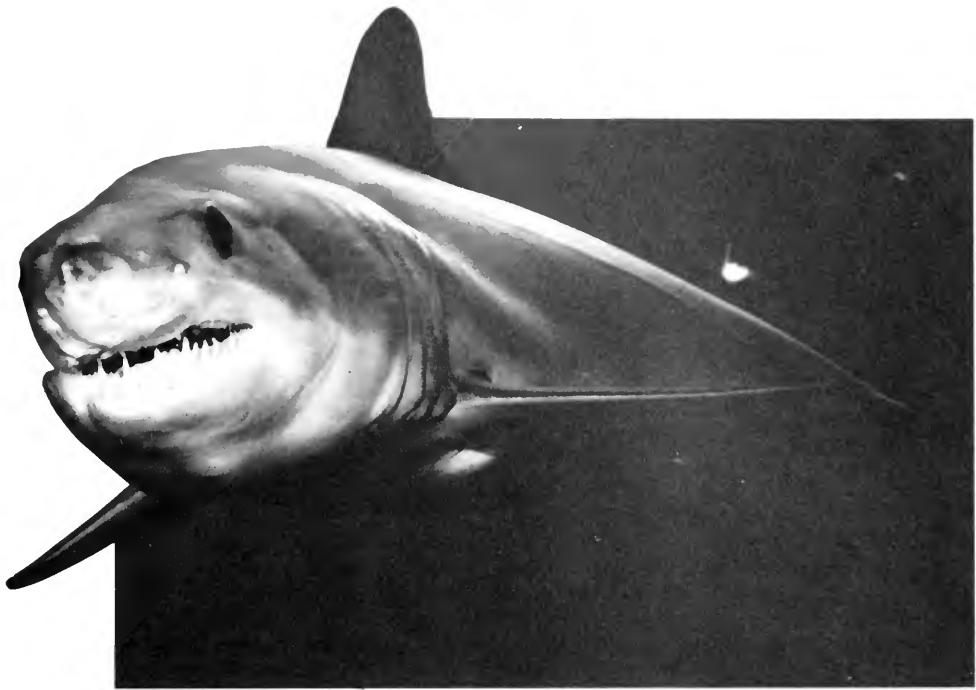
Use available spears and knives first to fend off the shark and attempt to wound the fish only as a last resort. Sharks often seem to react with increased vigor to efforts at sticking it with pointed objects.

Discretion should be used in making aggressive movements towards a shark. One that had not yet committed itself to attack might be "turned on" by such movements if interpreted by it as a threat. On the other hand, quick movements towards a shark close at hand might produce a desirable startle response.

Once contact has been made or is imminent, fight the shark as best you can. Hit it with your bare hands only as a last resort. Probing the shark's eyes especially and perhaps also its gills has often turned the tide. Startle responses which at least buy valuable time have been produced occasionally by such actions as shouting underwater or blowing bubbles. Do anything that comes to mind, for the seconds or minutes of time during which the shark might withdraw as a result could be sufficient to effect your rescue.

Most shark attacks produce wounds that are readily survivable. Bleeding should be controlled as quickly as possible — even before the victim has been brought ashore. Treatment by a physician is indicated even where wounds are relatively minor.

**From *Shark Attack*
by H. David Baldridge**



A mako, *Isurus oxyrinchus*, off San Diego, California. (Photo by Jeremiah S. Sullivan)

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Oceanography from Space, Vol. 24:3, Fall 1981 — Satellites already provide useful data and are likely to make important future contributions toward our understanding of the sea. This issue discusses their use in mapping wind patterns, chlorophyll concentration, sea ice movement, changes in climate, and sea-surface topography. The workings of a typical satellite are explained, as are some commercial applications of this new technology.

General Issue, Vol. 24:2, Summer 1981 — A wide variety of subjects is presented here, including the U.S. oceanographic experience in China, ventilation of aquatic plants, seabirds at sea, the origin of petroleum, the Panamanian sea-level canal, oil and gas exploration in the Gulf of Mexico, and the links between oceanography and prehistoric archaeology.

The Oceans as Waste Space?, Vol. 24:1, Spring 1981 — Whether we should use the oceans as a receptacle for waste or not is a question of much concern today. Topics in this issue include radioactive waste and sewage sludge disposal policies, problems of measuring pollutant effects, ocean outfalls, and mercury poisoning, as well as arguments for and against using the oceans for disposal of waste materials.

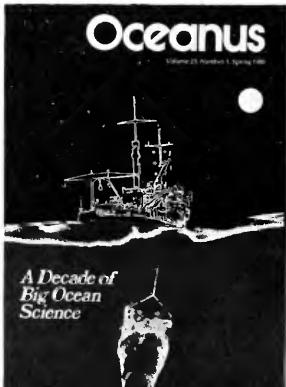
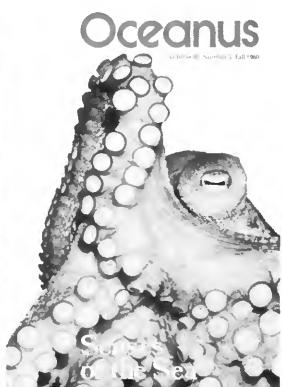
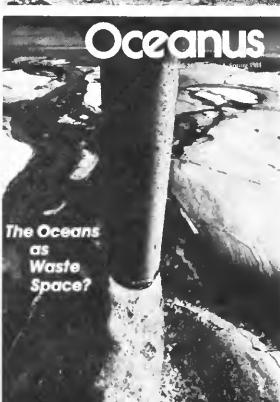
The Coast, Vol. 23:4, Winter 1980/81 — Celebrating the Year of the Coast, this issue is dedicated to the more than 80,000 miles of our nation's shorelines. Included are articles on barrier islands (federal policies and hazard mapping), storms and shoreline hazards, off-road vehicles on Cape Cod, the Apalachicola experiment, and coastal resource conservation and management.

Senses of the Sea, Vol. 23:3, Fall 1980 — Marine animals have complex sensory systems. Here we learn that lobsters can taste and smell, bacteria can sense their world magnetically, and some fish can sense electrically. We discover that octopuses have a sophisticated sense of equilibrium, and that some insects use the water surface to communicate. Underwater vision, hearing, and echolocation are also discussed.

General Issue, Vol. 23:2, Summer 1980 — A collection of articles on a range of topics, including: the dynamics of plankton distribution; submarine hydrothermal ore deposits; legal issues involved in drilling for oil on Georges Bank; and the study of hair-like cilia in marine organisms.

A Decade of Big Ocean Science, Vol. 23:1, Spring 1980 — As it has in other major branches of research, big science has become a powerful force in oceanography. The International Decade of Ocean Exploration is the case study. Eight articles examine scientific advances, management problems, political negotiations, and the attitudes of oceanographers toward the team approach.

Ocean Energy, Vol. 22:4, Winter 1979/80 — How much new energy can the oceans supply as conventional resources diminish? The authors in this issue say a great deal, but that most options—thermal and salinity gradients, currents, wind, waves, biomass, and tides—are long-term prospects with important social ramifications.



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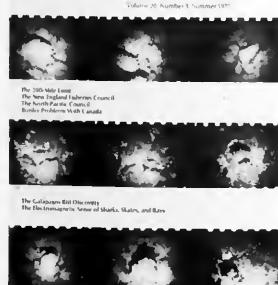
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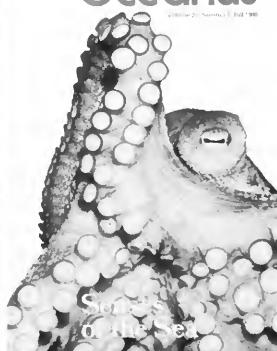
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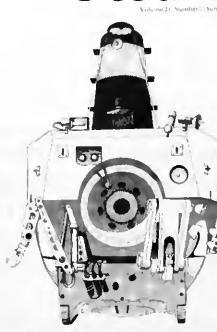
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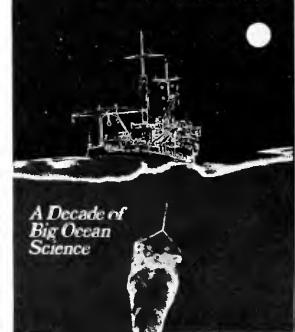
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Ocean/Continent Boundaries, Vol. 22:3, Fall 1979—Continental margins are no longer being studied for plate tectonics data alone, but are being analyzed in terms of oil and gas prospects. Articles deal with present hydrocarbon assessments, ancient sea-level changes that bear on petroleum formations, and a close-up of the geology of the North Atlantic, a current frontier of hydrocarbon exploration. Other topics include ophiolites, subduction zones, earthquakes, and the formation of a new ocean, the Red Sea.

General Issue, Vol. 22:2, Summer 1979—*Limited supply only.*

Harvesting the Sea, Vol. 22:1, Spring 1979—*Limited supply only.*

Oceans and Climate, Vol. 21:4, Fall 1978—This issue examines how the oceans interact with the atmosphere to affect our climate. Articles deal with the numerous problems involved in climate research, the El Niño phenomenon, past ice ages, how the ocean heat balance is determined, and the roles of carbon dioxide, ocean temperatures, and sea ice.

General Issue, Vol. 21:3, Summer 1978—The lead article looks at the future of deep-ocean drilling, which is at a critical juncture in its development. Another piece—heavily illustrated with sharp, clear micrographs—describes the role of the scanning electron microscope in marine science. Rounding out the issue are articles on helium isotopes, seagrasses, red tide and paralytic shellfish poisoning, and the green sea turtle of the Cayman Islands.

Marine Mammals, Vol. 21:2, Spring 1978—Attitudes toward marine mammals are changing worldwide. This phenomenon is appraised in the issue along with articles on the bowhead whale, the sea otter's interaction with man, behavioral aspects of the tuna/porpoise problem, strandings, a radio tag for big whales, and strategies for protecting habitats.

The Deep Sea, Vol. 21:1, Winter 1978—Over the last decade, scientists have become increasingly interested in the deep waters and sediments of the abyss. Articles in this issue discuss manganese nodules, the rain of particles from surface waters, sediment transport, population dynamics, mixing of sediments by organisms, deep-sea microbiology—and the possible threat to freedom of this kind of research posed by international negotiations.

Sound in the Sea, Vol. 20:2, Spring 1977—Beginning with a chronicle of man's use of ocean acoustics, this issue covers the use of acoustics in navigation, probing the ocean, penetrating the bottom, studying the behavior of whales, and in marine fisheries. In addition, there is an article on the military uses of acoustics in the era of nuclear submarines.

ISSUES OUT OF PRINT: **Sea-Floor Spreading**, Vol. 17:3, Winter 1974 **Air-Sea Interaction**, Vol. 17:4, Spring 1974 **Energy And The Sea**, Vol. 17:5, Summer 1974 **Marine Pollution**, Vol. 18:1, Fall 1974 **Food From The Sea**, Vol. 18:2, Winter 1975 **Deep-Sea Photography**, Vol. 18:3, Spring 1975 **The Southern Ocean**, Vol. 18:4, Summer 1975 **Seaward Expansion**, Vol. 19:1, Fall 1975 **Marine Biomedicine**, Vol. 19:2, Winter 1976 **Ocean Eddies**, Vol. 19:3, Spring 1976 **General Issue**, Vol. 19:4, Summer 1976 **Estuaries**, Vol. 19:5, Fall 1976 **High-Level Nuclear Wastes In The Seabed?** Vol. 20:1, Winter 1977 **Oil In Coastal Waters**, Vol. 20:4, Fall 1977

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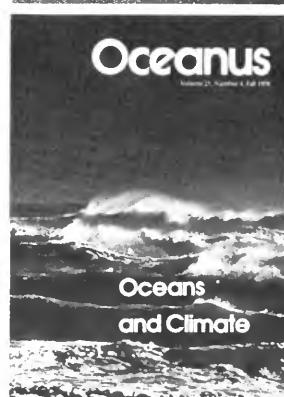


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